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Quantitative and Landscape Approaches to Amphibian Conservation

by Anthony J. Krzysik

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Foreword

The chapters reprinted in this report were published in *Status and Conservation of Midwestern Amphibians*, edited by Michael J. Lannoo, University of Iowa Press, Iowa City. The work was performed by Dr. Anthony J. Krzysik of the Ecological Processes Branch (CN-N), Installations Division (CN), Construction Engineering Research Laboratory (CERL). Dr. Harold E. Balbach is Chief CECER-CN-N, and Dr. John T. Bandy is Chief, CECER-CN. The Acting Director of CERL is Dr. Alan W. Moore.

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Contents

1 Introduction

Background

Natural resources and wildlife managers for Federal agency lands, including those dedicated to military training and testing missions, require environmental perceptions and decisionmaking at multiple scales and with implications that extend far beyond the local boundaries of the land the managers are responsible for. Although management of landscapes at the local installation level is still as important as it ever was, current perception for long-term ecological sustainability requires regional contexts and conservation efforts. Important technologies include:

- quantitative landscape approaches and Geographic Information Systems (GIS) capabilities,
- statistically valid sampling designs and data analysis methods for assessment and monitoring, and
- the use of ecological indicators of change to monitor natural, resource management, and mission-related disturbances; and ecosystem sustainability.

Specific taxonomic groups such as amphibians, birds, butterflies, ants, or carabid beetles, show promise to represent excellent taxa for tracking ecosystem, landscape, and possibly global ecological integrity.

This technical manuscript contains three peer-reviewed chapters from the book *Status and Conservation of Midwestern Amphibians*, M. J. Lannoo, editor, published by the University of Iowa Press in 1998. These chapters were brought together for the purpose of providing quantitative guidance and landscape perspectives to military land managers.

The chapter "5 Amphibians, Ecosystems, and Landscapes" describes a very fundamental and highly applicable approach to coarse-grained classification of ecosystems on a regional or continental basis and classifying taxa within the derived ecosystems. The example that is provided characterizes the Midwestern amphibian fauna and compares it to that of North America north of Mexico. Similarly, military wildlife managers can characterize prespecified or desired installation faunal elements and compare to regional or continental patterns. This approach was used to characterize the entire vertebrate fauna of the Marine

Corps Air Ground Combat Center in the south-central Mojave Desert and compare the distribution of this specific fauna to the entire Mojave and North America (Krzysik and Trumbull 1996*).

The chapter "41 Ecological Design and Analysis: Principles and Issues in Environmental Monitoring" provides guidance to both novice and experienced field biologist for designing and implementing ecological assessment or monitoring programs, and identifies important principles and issues in experimental design, field data collection, data management, and statistical analysis. The emphasis is on areas of common problems, pitfalls, sources of confusion, and misapplications. A rich and diverse source of recommended readings and references are provided. A recent review of this book said the chapter "would be useful for any student or professional initiating population studies and is worth the price of the book." (Stewart 1999§).

The chapter "42 Geographic Information Systems, Landscape Ecology, and Spatial Modeling" provides a readable introduction to the complex, but very valuable technologies and applications of Geographic Information Systems (GIS), cartography, landscape ecology and its metrics, and spatial modeling. A rich assortment of selected references are provided to extend the reader's knowledge base in specialized topics. GIS is one of the most important and practical resource management tools for land managers. Principles of GIS are developed in this section, stressing capabilities and applications, nature of input and output data, and the relative merits of raster and vector GIS. Fundamental concepts discussed in cartography include map scales, map projections, geographic coordinate systems, and thematic maps. The concepts and terminology of landscape ecology are introduced, stressing quantitative aspects of landscape patterns and issues of scale. Spatial modeling is introduced through a real-world example of producing a landscape density surface by the interpolation and smoothing of geographic field data of a highly fragmented desert tortoise population.

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* Krzysik, A.J. and V.L. Trumball. 1996. Biodiversity and Wildlife Management Plan: An Ecosystem Approach – Marine Corps Air Ground Combat Center, Twentynine Palms, California. Final Report, 400 pp.

§ Stewart, M.M. 1999. Book Reviews: "Status and Conservation of Midwestern Amphibians." *Copeia* 1999:536-538.

5

Amphibians, Ecosystems, and Landscapes

Anthony J. Krzysik

There is growing concern and empirical evidence that amphibians, even species that were considered historically to be abundant, are experiencing global population declines (Barinaga 1990; Blaustein and Wake 1990; Phillips 1990; Wyman 1990; Wake 1991). Phillips (1994) has written a popular book on the subject. Declines have been reported for the western (Hayes and Jennings 1986) and southwestern (Clarkson and Rorabaugh 1989) United States and the Caribbean (Hedges 1993). Lannoo et al. (1994) documented dramatic changes in an Iowa amphibian community between 1920 and the early 1990s.

Although amphibian declines have been discussed as a global phenomenon, there are regions of the globe that have not shown declines—the southeastern United States, Amazon basin, Andean slopes, central Africa, southeast Asia, Borneo, and the Philippines (Hedges 1993). Much of the decline in amphibian populations parallels comparable declines in other taxa and is the direct result of habitat loss, fragmentation, and degradation (including pollution) from anthropogenic activities, especially deforestation (e.g., Lowe 1985; Corn and Bury 1989; Dodd 1991; Hedges 1993). Reported declines have been associated with habitat loss or degradation (pollution), exotic fish or bullfrog introductions, acid deposition, disease, and increased ultraviolet (UV-B) radiation (ozone depletion). The stocking of trout (often by aircraft) in natural fishless alpine lakes of the western United States probably represents important predation on tadpoles. However, some amphibian population declines have occurred in relatively pristine areas that have not been impacted by humans (Heyer et al. 1988; Blaustein and Wake 1990; Czechura and Ingram 1990; Bradford 1991; Wake 1991; Crump et al. 1992; Carey 1993). Many declines remain a mystery, and an overall model including synergistic interactions and cumulative effects has not been proposed. The assessment of cumulative impacts are important for understanding environmental degradation (e.g., Johnston, Detenbeck, and Niemi 1990; Gosselink et al. 1990). Some researchers have urged caution and have noted that certain reports of amphibian declines may be explained as natural stochastic fluctuations (Pechmann et al. 1991).

There are at least four important reasons for considering a comprehensive global-scale amphibian monitoring program:

1. Hypothesis testing—are there declines in amphibian populations on local, regional, national, and global scales? What are the taxonomic and scale issues? What are the causes with respect to taxa, scale, and environmental, ecological, or natural history requirements? Are the declines relevant to order (i.e., only frogs), specific families, genera, species, or populations? To what extent are amphibian declines global, national, regional, or local issues? Is there one cause for the decline, or are there few or many causes? What are the implications for synergisms and cumulative effects?

2. Amphibian species are strongly associated with their habitats (ecosystems), and some species requirements are highly stenotopic (i.e., have narrow environmental requirements). A large majority of amphibians require landscape mosaics of two or more

ecosystems and spatial habitat integrity (i.e., dispersal corridors) to complete life history requirements. This implies sensitivity to habitat fragmentation. Therefore, amphibians represent excellent ecological indicators or barometers of the ecological condition of landscapes. A global monitoring program for amphibian populations and communities in an ecoregional context represents an integral component of spatial and temporal trend analysis and risk assessment in monitoring the ecological integrity of global ecosystems.

3. There are legal mandates under the Federal Endangered Species Act, state legislation, and international statutes and agreements. Many amphibian species are already listed on international, federal, and state levels as threatened, endangered, or sensitive (see Lannoo, Introduction, this volume).

4. There are the conservation implications of taxa that are rare or possess very limited distributions.

The landscape ecology approach and spatial technologies in the framework of Geographic Information Systems (GIS) (e.g., remote sensing and spatial analysis/modeling) represent powerful tools for monitoring and modeling the distribution, density patterns, and metapopulation dynamics of amphibian populations. Additionally, GIS can be instrumental in extending these data into other applications relevant to the conservation biology of amphibians. (See Krzysik [Chpt. 42, this volume] for an introduction to, and examples of, GIS, landscape ecology, and spatial modeling.)

Landscapes and Ecosystem Classification

It is important to distinguish between scale, landscapes, and ecological hierarchies. Scale is defined by spatial extent (see Krzysik, Chpt. 42, this volume, Table 42-2). Landscape can refer to two attributes: spatial scale (which inherently includes pattern) or spatial pattern (at any scale). Landscape scales are on the order of 1 to 10,000 square kilometers, while landscape patterns refer to the spatial context of landscape mosaics and environmental gradients (see Krzysik, Chpt. 42, this volume).

Ecological hierarchies represent the hierarchical organization of biological systems, consisting of genes/populations, communities/ecosystems, ecoregions, and the globe. In this series the higher hierarchy is comprised of elements from the next lower one. Species and subspecies consist of one, few, or many populations defined by genetic structure in a spatial/temporal context. Species are not evenly distributed in the landscape but respond to environmental/ecological mosaics and gradients (i.e., habitat selection). Populations of a species or subspecies on the landscape can be classified on the basis of gene flow as panmictic, metapopulations, or isolated. Panmictic refers to potentially freely and randomly interbreeding individuals in a single gene pool (approximately at one genetic exchange per generation; reviewed in Lande and Barrowclough 1987). A metapopulation represents the situation where, as spatially explicit populations become extinct, colonization occurs from other occupied patches, and a long-term equilibrium is possible (Levins 1969; Gilpin and Hanski 1991). However, a more recent review has challenged some of the assumptions of traditional metapopulation dynamics and stresses the need for a better understanding of the spatial scales and the ecological and genetic processes operating on local populations (Hastings and Harrison 1994). Isolated populations have no genetic exchange, and therefore there is the potential for either genetic divergence or extinction (Franklin 1980; Soulé 1980, 1987).

Communities are species/population assemblages characterized by composition, functions, and interactions (e.g., competition, predation, mutualism, and parasitism). Communities can be defined in a specific spatial/temporal context at any scale. An ecosystem consists of one or more communities within a spatial/temporal context of any scale, characterized by its processes and the flow (transfer) of energy, materials, and organisms into and out of the system. Ecoregions are global-scale (continental) landscapes spatially distinct from one another by their climate, physiography, hydrology, and biota.

Ecologists, geographers, and philosophers will always argue over ecological classifications and boundaries. This is not surprising, because nature abhors classifications and boundaries. Nevertheless, even in the context of the reality of the spatial complexity of biological, physical, and chemical gradients/mosaics and temporal dynamics, in making ecologically responsible land-use and management decisions it is necessary to develop ecosystem classifications and boundaries in order to assess and monitor natural resources and to conserve biodiversity. For more information, see the review by Bailey (1996).

This chapter introduces a systematic hierarchical approach to the classification of ecosystems. Although ecosystems are not spatially static but represent dynamic trajectories, ecosystem classifications portray a convenient spatial and functional reality. Terminology must first be introduced. The environment is the complete spatial and temporal context of biotic and abiotic attributes. Environmental attribute sets (EASs) are eleven sets of environmental attributes that completely and explicitly define the environment at any scale. Environmental attributes are parameter sets that define the environment (e.g., temperature, precipitation, topography, streams, roads, and vertebrates). Environmental parameters (variables) are specific quantifiable variables that define attributes (e.g., maximum or minimum or variance of daily temperature, amount of rainfall per month, elevation, percent slope, number of second-order streams per square kilometer, average instream flow rate, length of secondary roads per square kilometer, number of species of vertebrates, and density of carnivores per square kilometer).

Table 5-1 presents the eleven EASs. Note that this is the baseline of a hierarchy (e.g., the coarsest scale) that characterizes ecosystems and determines their identification (or habitat gestalt), composition, and processes. Note also that the EASs are closely related and interdependent. For the objectives of a given analysis or project, each EAS can consist of a single parameter or multiple parameters, and some EASs are superfluous or may be ignored. The system is valid at any extent (scale) and at any grain (resolution), and the details of hierarchies, EASs, and parameters considered are user relevant. I will briefly discuss the eleven EASs.

Table 5-1. Environmental attribute sets (EASs) for any extent and grain

1.	Climate
2.	Geomorphology-Geology
3.	Hydrology-Hydrography
4.	Soils-Substrate Texture
5.	Plants
6.	Microbes
7.	Animals
8.	Disturbance Regimes
9.	Anthropogenic Disturbance
10.	Biogeography
11.	Stochasticity

Climate

The climate of a region determines the nature of its landscape and ecosystems. Climate is determined by spatial location on earth relative to the energy flux of the sun (intensity and duration), proximity to large bodies of water (e.g., oceans), topography (e.g., elevation or mountain rain shadow), prevailing winds, and ocean currents. Therefore, the most important parameters include latitude, longitude, and elevation, which in turn determine temperature, precipitation, humidity, and actual and potential evapotranspiration. Temperature extremes (maximum, minimum, or some measure of temperature regimes) and the seasonal distribution (variance and predictability) of rainfall are more important predictors of biotic responses than averages. A single variable representing energy flux—potential evapotranspiration—was successful at predicting 80 to 93 percent of the variability in species richness of amphibians, reptiles, birds, and mammals in North America north of Mexico (Currie 1991; in contrast, see Brodman, Chpt. 4, this volume).

Continental-scale climatic parameters are directly associated with floral and faunal patterns (i.e., ecoregions or biomes). However, microclimates are undoubtedly important for amphibians, invertebrates, and other taxa, especially when considering moisture gradients. The next three EASs that will be discussed directly influence the development of microclimates.

Geomorphology-Geology

Geomorphology, or physiography, defines landform and its geology and is applicable at any scale, from continental-scale physiographic provinces and geological formations to microtopography. The three main physiographic provinces of the Southeast—mountains, piedmont, and coastal plain—exemplify biological differentiation, well illustrated by the regions, herpetofauna, including subspecies. Topography is important for the distribution/abundance patterns of amphibians. Important ecosystem parameters are elevation, topographic complexity, percent slope, slope aspect, depressions for pools of rainwater, and geological outcrops. Important habitat elements for salamanders include flaking sandstone cliffs for the green salamander (*Aneides aeneus*), flaking shale in moist forests for the longtail salamander (*Eurycea longicauda*), and cave sites for the cave salamander (*E. lucifuga*).

Hydrology-Hydrography

Hydrology represents wetland, aquatic, and riparian ecosystems. This is an important EAS not only for amphibians but also for landscape and regional biodiversity. Hydrology readily lends itself to hierarchical classification (e.g., Cowardin et al. 1979). Important hierarchical attributes include:

1. Surface waters
   a. Lentic—stationary waters: lakes, ponds, sloughs, quiet pools of streams, temporary pools (including floodplains)
   b. Lotic—running waters: rivers and streams, including springs. Lotic systems are readily classified into stream orders (e.g., Strahler, 1964).
   a1 or b1. Perennial waters—permanent water
   a2 or b2. Intermittent waters—predictable seasonal water, present at least several months to most of the year, generally absent in midsummer through fall
   a3 or b3. Ephemeral waters—unpredictable waters of shorter duration, lasting from several hours—for example, in desert washes—to several weeks and usually less than one or two months. Temporary waters are probably highly significant landscape elements, but their ecology is poorly known (Williams 1987). Vernal pools are important landscape elements, particularly in Mediterranean regions of the world, that are endangered ecosystems (Zedler 1987).
2. Subsurface or subterranean waters—underground ecosystems that are poorly known. The unexpected fauna of the hyporheos is just beginning to be appreciated (reviewed in Ward 1992).

Riparian ecosystems are classified according to their association with perennial, intermittent, or ephemeral waters as hydroriparian, mesoriparian, and xeroriparian, respectively.

Soils-Substrate Texture

Soil classes (reflecting their physical, chemical, and biological properties), texture, organic content, and soil depth are important EASs characterizing ecosystems. Soil types determine moisture capacity, infiltration, erosion potential, suitability for burrowing, and vegetation types. Because the technical definition of soil is rock that is exposed to weathering (Jenny 1980; Huggett 1995), substrate texture is a component of soil classification. Soil texture directly determines flora and fauna species compositions based on the relative distribution of particle sizes: clay, silt, sands, gravels, cobbles, and boulders (Table 5-2 presents a useful classification for soil or substrate texture).

Plants, Microbes, and Animals

Because of their importance, plants, microbes, and animals were classified into three EASs, but they just as effectively could have been considered as three high-

Table 5-2. Soil or substrate texture classification

Texture Class	Particle Size Range (mm)	Coarse Classification*
Clay	0.00025 – < 0.004	
Silt	0.004 – < 0.0625	
Fine sand	0.0625 – < 0.5	Fine
Coarse sand	0.5 – < 4	Sand
Fine gravel	4 – < 15	Fine gravel
Coarse gravel	15 – < 75	Coarse gravel
Cobbles	75 – < 300	
Small boulders	300 – < 600	Rocks
Medium boulders	600 – < 1200	
Large boulders	1200 – < 2400	
Very large boulders	> 2400	Boulders

*A coarse classification may be useful for some applications and with little practice can rapidly be conducted by eye without actual measurements.

order attributes in a single EAS, the biological environment. Plants, microbes, and animals are interdependent and interact among themselves and with other EASs, which are also closely interdependent and which influence one another to a large extent. The biological environment determines the specific structure (including composition), dynamics, and patterns of competition, predation, mutualism, parasitism, and disease/pathogens in an ecosystem classification framework.

Disturbance Regimes

Natural disturbance regimes influence the seven EASs above them in Table 5-1, and both ecosystem processes and the maintenance of biodiversity are dependent on them. Examples of attributes include flood pulses, fire regimes, storms and windthrows, and pest and pathogen outbreaks. These are usually modeled as stochastic processes, and specific estimated parameters (often empirically derived) are used for frequency, extent (spatial), duration (temporal), and intensity. Global events on geological time scales, such as volcanism and asteroids, are not considered in this category.

Anthropogenic Disturbance

Human dominance of landscapes—with its inevitable habitat conversions, destruction, and degradations, from local to global scales—is geologically and evolutionarily a recent phenomenon, but it is already challenging the intensity and scale of the two greatest mass extinctions the planet has faced: those at the Permian-Triassic and Cretaceous-Tertiary boundaries (Ward 1994). Quantitative measures of human presence and disturbance to the landscape are important for amphibian monitoring and include road density (classified by interstates, secondary roads, rural dirt roads, jeep trails, etc.), fractal dimension, contagion, land cover type, ecosystem/habitat areas, fragmentation, connectivity, adjacent ecosystems, and landscape pattern. Langton (1989) discusses the effects of roads on amphibians. Various metrics for quantification are discussed in Krzysik (Chpt. 42, this volume).

Biogeography and Stochasticity

Species distribution and density patterns from local to global scales are primarily dependent on the EASs discussed above. However, several other factors are also responsible and in specific circumstances may be important, but they are difficult to quantify and are included as EASs for completeness. These attributes represent biogeography (spacial, temporal, and historical factors) and stochasticity, which represents random unpredictable events, including catastrophes such as volcanos, earthquakes, meteors/asteroids, and extreme cases of the natural disturbance regimes discussed above.

Amphibians on the Landscape

I constructed a baseline classification of ecosystems relevant to amphibian ecology and natural history requirements. The classification was based mainly on hydrology but also reflected topography (see Table 5-3). It is important to note that there is a substantial ecological difference and implications between riparian zones and the presence of both aquatic and terrestrial habitats. Riparian zones have their own ecological identity based on structure, function, and processes and are characterized by steep moisture, physical, and chemical environmental gradients. The functionality of these ecosystems, as well as the response of biological organisms to them, is unique and cannot be considered as either aquatic or terrestrial habitat or both. Species that are riparian specialists require the environmental, biological, and spatial contexts of this water-land interface. Although riparian systems represent a wide variety and complexity of classes (mainly dependent on region and geomorphology), they remain unique in the landscape and should be classified as such (Gregory et al. 1991; Franklin 1992; Malanson 1993). A federal symposium on the value of riparian habitats was instrumental in initiating a great deal of interest and research in these previously ignored ecosystems (Johnson and Jones 1977). If riparian zones are degraded (by humans or cattle), riparian species are dramatically affected, but species requiring aquatic or both terrestrial and aquatic habitats may not be affected. It is well documented that the ecological integrity of riparian zones directly affects water quality, instream flows, and flooding regimes (Karr and Schlosser 1978; Osborne and Wiley 1988; Johnston, Detenbeck, and Niemi 1990; Schlosser 1991; Becker and Neitzel 1992).

I matched the ecosystem classification of Table 5-3 with all of the amphibian genera in North America north of Mexico (Collins 1990; Table 5-4). Note that three genera in the Midwest fauna (*Desmognathus, Eurycea, Gyrinophilus*) include species outside of the Midwest that have different ecosystem requirements. A subset of these data consisted of genera occurring in the midwestern states included here. Amphibian genera represent major ecological adaptive themes (e.g., Inger 1958) and therefore provide a foundation to characterize and monitor natural history requirements in the

Table 5-3. General ecosystem classes important to amphibians. See text for explanation of terminology.

Terrestrial			
Aquatic	Surface	Lentic	Perennial
			Intermittent
			Ephemeral
		Lotic	Perennial
			Intermittent
			Ephemeral
	Subsurface		
Riparian		Lentic	Perennial
			Intermittent
			Ephemeral
		Lotic	Perennial
			Intermittent
			Ephemeral
Wetlands			Marshes, fens, bogs
			Swamps, floodplains

context of environmental trends and habitat condition, including landscape-scale ecosystem requirements, spatial patterns, and temporal trends. However, the use of subspecies (or metapopulations or gene pools) is the preferred approach, because populations are the inherent units in natural selection and fitness, providing the adaptations for exploiting their spatial environmental resources—ecosystem requirements (specialized ecological adaptations). Additionally, a further hierarchical finer resolution of the ecosystem classification presented here provides a foundation for amphibian conservation. Indeed, analysis at one hierarchical level provides the data for more detailed ecosystem classification.

Figure 5-1 shows that most salamanders are completely terrestrial or aquatic or require the ecotone (interface) between these ecosystems. Most anurans require both terrestrial and aquatic ecosystems in the landscape. There are no anurans in our fauna that are completely aquatic or found in subterranean waters, and only two genera are completely terrestrial. These data suggest that anurans would be more susceptible to landscape fragmentation than are salamanders because they are more dependent on landscape mosaics, the patterns developed by two or more ecosystem types.

Although thirty-one ecosystem combinations are possible in Table 5-3 (sixteen single classes and fifteen when pairing terrestrial with one of the other fifteen classes), only eleven ecosystem classes were required to classify on a baseline scale the ecology and natural history requirements of all amphibian genera (Table 5-5). Figure 5-2 shows the relationships of the United States and Canadian (USC) amphibian fauna to the eight single ecosystem classes, and Figure 5-3 shows the comparable data for the Midwest fauna. Trends in the Midwest fauna are in general comparable to trends in the USC fauna. The major differences are that the Midwest has no completely terrestrial anurans (the two terrestrial genera are tropical-subtropical), has a higher proportion of completely aquatic salamanders, is less represented by subterranean forms, and has a higher proportion of wetland (including riparian-lentic) anurans. Figures 5-4 and 5-5 show comparable data on the respective faunas that require both terrestrial and aquatic ecosystems to complete their life histories. Again, the midwestern fauna reflects the USC fauna, with the main differences being that a higher proportion of USC anurans rely on ephemeral breeding pools than do those in the Midwest (reflecting western adaptations to arid and semi-arid

Table 5-4. Legend

TER	Terrestrial
AQ-LE	Aquatic-Lentic-Perennial Waters; may include marsh habitat
RIP-LE	Riparian-Lentic-Perennial Waters
AQ-LO	Aquatic-Lotic-Perennial Waters
RIP-LO	Riparian-Lotic-Perennial Waters; includes springs
SUB	Subsurface, Subterranean Waters
WET-M	Wetlands-Marshes, Fens, Bogs
WET-S	Wetlands-Swamps, Floodplains
LE-P	Terrestrial and Aquatic Lentic-Perennial Waters
LE-IE	Terrestrial and Aquatic Lentic-Intermittent or Ephemeral Waters; may include floodplain pools
LO-PIE	Terrestrial and Aquatic Lotic-Perennial, Intermittent, or Ephemeral Waters

Table 5-4. The ecosystem classifications of Table 5-3 matched with the amphibian genera in North America north of Mexico

Genus	TER	AQ-LE	RIP-LE	AQ-LO	RIP-LO	SUB	WET-M	WET-S	LE-P	LE-IE
Ambystoma									Mid, C	Mid, C
Amphiuma		Mid		Mid						
Aneides	Mid, C									
Batrachoseps	US, C				US, C					
Cryptobranchus				Mid						
Desmognathus	US		US		Mid, C			US		
Dicamptodon					US, C					
Ensatina	US, C									
Eurycea	Mid			US	Mid, C	US				
Gyrinophilus					Mid, C	US				
Haideotriton						US				
Hemidactylium	Mid, C									
Hydromantes	US				US					
Leurognathus				US						
Necturus		Mid, C		Mid, C						
Notophthalmus									Mid, C	
Phaeognathus	US									
Plethodon	Mid, C									
Pseudobranchus		US		US						
Pseudotriton			Mid		Mid			Mid		
Rhyacotriton					US					
Siren		Mid		Mid						
Stereochilus			US		US			US		
Taricha									US, C	US, C
Typhlomolge						US				
Typhlotriton						Mid				
Acris			Mid, C		Mid, C					
Ascaphus					US, C					
Bufo									Mid, C	Mid, C
Eleutherodactylus	US									
Gastrophryne										Mid
Hyla								Mid, C	Mid, C	Mid, C
Hypopachus										US
Leptodactylus										US
Osteopilus									US	US
Pseudacris								Mid, C	Mid, C	Mid, C
Pternohyla										US
Rana			Mid, C		Mid, C		Mid, C	Mid, C	Mid, C	Mid, C
Rhinophrynus										US
Scaphiopus									Mid	Mid
Smilisca									US	US
Spea										Mid, C

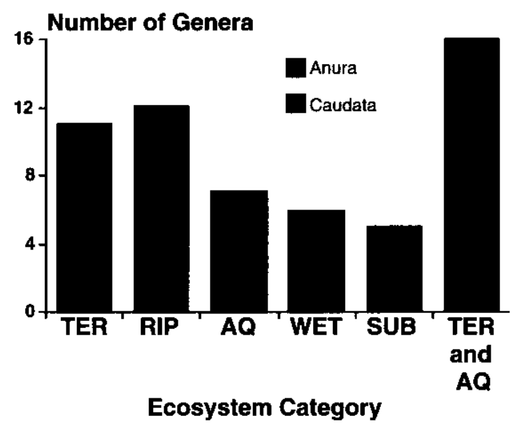

Figure 5-1. Distribution of United States and Canadian amphibian genera in six general ecosystem classes. For explanation of abbreviations, see Table 5-4. Note that the last class is the only one that consists of two ecosystem classes—terrestrial and aquatic.

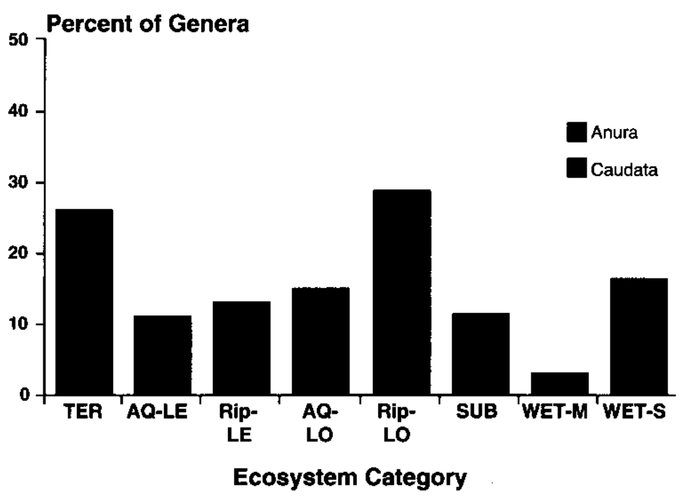

Figure 5-2. Percent of United States and Canadian amphibian genera classified by ecosystem requirements. For explanation of abbreviations and for the specific requirements of each genus, see Table 5-4.

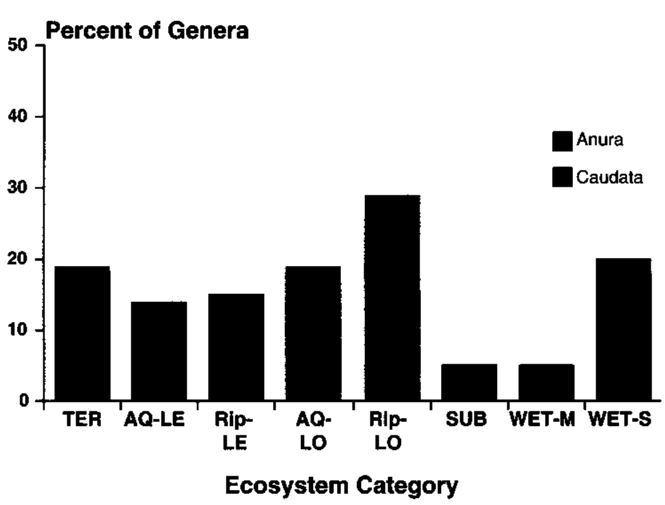

Figure 5-3. Percent of Midwest amphibian genera classified by ecosystem requirements. For explanation of abbreviations and for the specific requirements of each genus, see Table 5-4.

landscapes) and the importance of Pacific coast streams as breeding sites for some *Taricha* species.

The classification of each subspecies based on a finer resolution ecosystem hierarchy, including regional differences, would be most illuminating for designing a national monitoring program. Some genera are species rich. Although some of this diversity represents allopatric geographical divergence, much of it undoubtedly underlies environmental adaptations that would enrich the hierarchical classes of Table 5-5 and provide more detailed environmental requirements and ecosystem relationships. Species-rich genera based on Collins (1990), not including recognized subspecies, are *Plethodon* (forty-two), *Rana* (twenty-four), *Bufo* (eighteen), *Ambystoma* (fourteen), *Pseudacris* (thirteen), *Desmognathus* (twelve), *Eurycea* (twelve), *Hyla* (ten), and *Batrachoseps* (ten). *Batrachoseps* and *Ensatina* (only one species with seven subspecies) are two taxa that are currently being revised, and undoubtedly their richness will increase.

Assessing and Monitoring Amphibian Populations with GIS

Below is an outline of the potentials of GIS for assessing and monitoring amphibian/ecosystem parameters and analyzing and modeling their relationships.

1. Database management
    a. Spatial database needs and analytical requirements
    b. Distribution and abundance data for amphibian populations
    c. Ecosystem attributes (Tables 5-3, 5-4) and hierarchical extensions

Table 5-5. Eleven ecosystem classes important to amphibian ecology and natural history. See text for explanation of terminology.

Terrestrial			
1			
		Lentic	Perennial
2			
Aquatic	Surface		
		Lotic	Perennial
3			
	Subsurface		
4			
		Lentic	Perennial (intermittent)
5			
Riparian			
		Lotic	Perennial (intermittent)
6			
		Marshes, fens, bogs	
7			
Wetlands			
		Swamps, floodplains	
8			
			Perennial
9			
		Lentic	
			Intermittent, ephemeral
10			
Terrestrial and Aquatic			
			Perennial, intermittent
11		Lotic	
			Ephemeral

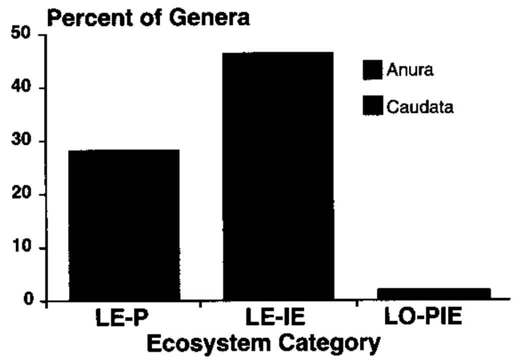

Figure 5-4. Percent of United States and Canadian amphibian genera needing both terrestrial and aquatic ecosystems. For explanation of abbreviations and for the specific requirements of each genus, see Table 5-4.

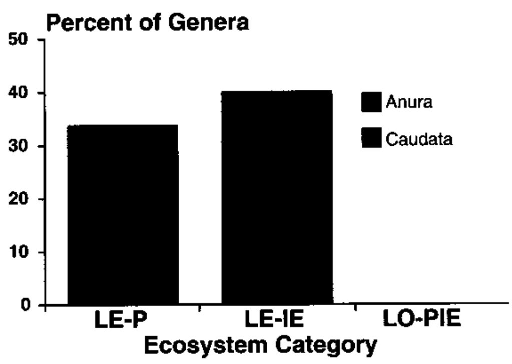

Figure 5-5. Percent of Midwest amphibian genera requiring both terrestrial and aquatic ecosystems. For explanation of abbreviations and for the specific requirements of each genus, see Table 5-4.

2. Coverage manipulations and transformations
    a. Transformations of scale—extent and grain
    b. Changes in cartographic projection
    c. Georeferencing and classification of thematic maps
    d. Merging of thematic maps
3. Identification of specific ecosystems
    a. Selection of specified ecosystems—absolute or probability based
    b. Deletion of specific ecosystems
    c. Ranking of ecosystems
4. Disturbance
    a. Natural regimes
    b. Anthropogenic
5. Spatial contexts of ecosystems
    a. Metrics—size, shape, and condition
    b. Metrics—patterns, mosaics, fragmentation, connectivity, density, association, distance, texture, and similarity indices
    c. Ordinations, classifications—environmental gradients
6. Temporal contexts of ecosystems
    a. Monitoring ecosystem trends
    b. Monitoring spatial contexts
7. Modeling
    a. Species-habitat (environment) relationships
    b. Metapopulation dynamics in spatial and temporal contexts
    c. Natural and anthropogenic disturbances in spatial and temporal contexts
8. Sampling
    a. Develop sampling design
    b. Select specific sampling sites
    c. Model validity, efficiency, and economy
9. Outputs
    a. Visual displays, maps, tabular output, and magnetic/electronic data
    b. Identification of data needs
    c. Protection, conservation, and management needs

Summary

There is growing concern that amphibian populations are declining from local to global scales. A robust hierarchical ecosystem classification system is presented that is applicable at any scale and resolution (more correctly, extent and grain in landscape ecology terminology). From this conception, a baseline ecosystem classification is developed that is relevant to amphibian ecology and conservation. Although there are many ecosystem combinations possible in this classification, including combinations requiring two or more ecosystems, only eleven ecosystem classes were required to classify on a baseline scale the natural history requirements of all the amphibian genera of North America north of Mexico. Amphibian genera represent major ecological adaptive themes and therefore provide a foundation to characterize and monitor natural history requirements in the context of environmental trends and habitat condition. General trends for ecosystem requirements in this fauna are discussed, including a comparison with genera occurring in the Midwest. Trends in the Midwest fauna are

in general comparable to the continental fauna. The major differences, based on genera, are that the Midwest: (1) has no completely terrestrial anurans, (2) has a higher proportion of completely aquatic salamanders, (3) is less represented by subterranean forms, and (4) has a higher proportion of wetland (including riparian-lentic) anurans. The continental fauna has a higher proportion of anurans that rely on ephemeral breeding pools, reflecting western adaptations to arid and semiarid landscapes.

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Ecological Design and Analysis: Principles and Issues in Environmental Monitoring

Anthony J. Krzysik

The purpose of this chapter is to identify some important principles and issues in areas that are relevant to field biologists and ecologists and to researchers or environmental managers who are designing and implementing ecological assessment or monitoring programs. It is not meant to provide an introduction, or a comprehensive review, of experimental design or statistical analysis. The principal goal of the chapter is to discuss areas of common pitfalls, confusion, misunderstandings, misapplications, and the typical sources of statistical errors. The intended audience is both the novice and the experienced practitioner. Extensive references to the literature are provided, and these, along with my personal experiences, are synthesized. Although original reference sources are given, the major emphasis has been on identifying practical and useful literature to provide the reader with fundamentals and some examples in the science (some would say art) of experimental design and statistical analysis.

A review of research designs and data analysis, as well as inventory methods relevant to monitoring amphibian populations, is provided by Heyer et al. (1994). Introductory overviews of ecological monitoring are found in Clarke (1986), Goldsmith (1991), and Spellerberg (1991).

Issues in Statistical Analysis

Approaches

Statistical analysis consists of at least six general approaches.

Estimation. A common approach is estimating the mean of a population and, just as important (usually more so), an associated measure of the precision of the estimate. (Population in this chapter will be used in a statistical sense and refers to a collection of observations, measurements, or individuals. In this context it can also refer to a treatment or control group.) The precision in the estimate depends on the inherent variability in the population and the sample size used to estimate the statistic under investigation. Statistical precision is called error and is expressed as standard deviation, standard error, confidence interval, or coefficient of variation.

Inference. Inference, or hypothesis testing, is the most frequently associated and best-known approach for the rationale of statistical analysis. Inference helps the investigator decide if the observed difference in a test statistic (e.g., mean) between two or more populations is due to chance at some a priori set probability. The question is posed as a null hypothesis to falsify (null hypothesis: populations are homogeneous). If there is no difference between two or more populations, what is the probability of selecting samples with differences as large as or larger than those observed? This probability is the familiar p-value, or α. If this probability is small, then one concludes that the differences are unlikely to be due to chance, and there is a statistically significant difference in the populations (null hypothesis rejected) at the p-level. If the probability is large (observed differences may be due to chance alone), then either the populations are homogeneous at the p-level or the statistical power of the test was too low (i.e., some combination of small sample size, high natural variability, or the "difference" selected to assess significance was too small). It is imperative to remember that the null hypothesis can never be proved correct but can only be rejected with a known risk of being wrong.

Exploratory Data Analysis. Exploratory data analysis (EDA) is an important class of statistical analysis that has not been fully appreciated, despite the excellent technical foundation laid by Tukey (1977). EDA has also been called Initial Data Analysis (IDA) by Chatfield (1988), who concludes that the process is indispensable and required by the statistician to get a feeling for the data. EDA is intended to:

1. check the quality of the data, including missing observations, outliers, high variance, or noise
2. compare controls and treatments and to assess the relative magnitude of differences
3. examine patterns in the data
4. calculate and examine descriptive and summary statistics
5. examine and test for suitability of design and analysis assumptions (e.g., parametric, multivariate normality, independence, stratification justification)
6. evaluate the need for data transformations (e.g., to fit parametric assumptions, especially homoscedasticity [homogeneous variances]) or rescaling of data
7. provide an aid for statistical model formulation and for determining or refining final statistical analyses methods

All of these are important to EDA, and their relative merits directly depend on the specific nature of the project or database in question. The routine use of EDA has become a current reality because of the power of modern microcomputers and the availability of interactive graphics and extensive graphics output options in microcomputer statistical software packages (e.g., SAS, S-PLUS, SPSS, SYSTAT). All of these packages are excellent and come with excellent documentation. Comprehensive guides for using S-PLUS (Venables and Ripley 1994) and SYSTAT (Wilkinson et al. 1996) are available. SAS is only available by license, making it accessible to universities but too expensive for individuals and most federal research facilities. While there are other good statistical packages available, I am most familiar with these four.

Interactive graphics enable one to rapidly examine data patterns and trends from scatterplots of raw data, transformed or rescaled data, or residuals; references include Chambers et al. (1983) and Cleveland (1993). An important procedure, available in all four of the above statistical packages, is the scatterplot matrix. If you have ten variables in your study and in your EDA you want to investigate their relationships to each other, the scatterplot matrix routine produces a single plot containing 100 subplots of each combination of the ten variable pairs. The plots above the diagonal are the same as the plots below the diagonal, except that the ordinates and abscissas of all paired variables are interchanged.

The importance of EDA using graphical displays, scatterplots, and visualizing data techniques is exemplified in a most remarkable example discussed by Cleveland (1993). Minnesota agronomists in the early 1930s conducted a field experiment on barley yields at six study plots. The data were subsequently analyzed, reanalyzed, and used as examples, even into the 1960s and 1970s. Sir Ronald Fisher, who developed the foundations of modern statistics, analyzed the data and even used them as an example in his classic book on experimental design (Fisher 1935); Fisher's three seminal books, *Statistical Methods for Research Workers* (1925), *The Design of Experiments* (1935), and *Statistical Methods and Scientific Inference* (1956) were published as a single book, entitled *Statistical Methods, Experimental Design, and Scientific Inference,* in 1990 by Oxford University Press. The statisticians who examined the data consistently concluded that five of the six plots showed a barley yield decrease between 1931 and 1932, while the other plot showed an increase. The use of visualizing data techniques and scatterplots clearly demonstrated that there was a major error in the data set; the study plot with the aberrant trend had its years mistakenly interchanged prior to all subsequent analyses. When this error was corrected, all plots showed remarkable consistency in yield decrease between 1931 and 1932.

In addition to the references noted above, important references on EDA are Ehrenberg (1975), Erickson and Nosanchuk (1977), McNeil (1977), Velleman and Hoaglin (1981), Hoaglin et al. (1983, 1985, 1991), and Chatfield (1985).

Descriptive. The distinction between EDA and descriptive statistics is academic because, for practical purposes, descriptive statistics are an important component of EDA. Descriptive statistics are generally summary statistics for all of the primary parameters or variables in the project, generally stratified by spatial, temporal, or user-defined classes. Summary statistics are provided by all statistical analysis packages. An important part of this category is the art and science of data display and graphics presentations. A foundation for the philosophy and techniques of data display has been the work of Tufte

(1983, 1990). Practical guidance for using graphics effectively can be found in Chambers et al. (1983) and Cleveland (1993). The four statistical packages mentioned earlier also provide advice on producing and displaying graphics. Two high-quality scientific graphics packages that have excellent graphics capabilities and documentation are Axum and SigmaPlot. There is even a book available for providing guidance for using SigmaPlot (Charland 1995).

Modeling. Modeling represents the efforts to verify whether experimentally derived data fit specific mathematical models related to biological, physical, geological, or chemical phenomena or processes. The most common example in statistics is linear regression: do the data fit a straight line? Of course, any kind of polynomial curves in any dimensions can be equivalently modeled, but with much more difficulty. Krzysik (Chpt. 42, this volume) discusses the modeling of "thin-plate spline functions" to interpolate and smooth a surface fit to three-dimensional field data points of estimated population densities.

There are four main strategies in model building: model formulation, model estimation or fitting, sensitivity analysis, and model validation. Model validation includes the familiar:

Experimental data = mathematical model + residuals

For further analysis, the residuals can be subjected to standardization (homogeneous variances), their distribution can be examined by using probability plots, they can be plotted against selected variables, or they can be subjected to additional modeling. The analysis of residuals may provide valuable insight into an important facet or unexpected behavior of the model. More details of statistical modeling are available in Daniel and Wood (1980) and Gilchrist (1984). See also the subsection on Parametric Statistics (below).

Spatial Analysis. Spatial analysis has developed independently from mainstream statistics and has employed its own terminology. Spatial statistics, once the domain of mainframe and minicomputer workstations, is rapidly gaining popularity with the growing use of Geographic Information Systems (GIS; Krzysik, Chpt. 42, this volume) and the availability of high-power microcomputers. Within the next year or two, spatial analysis modules will be available for most popular microcomputer statistics packages. A module for S-PLUS has already been released. Krzysik (Chpt. 42, this volume) presents a summary of interpolation and smoothing methods and a survey of the literature.

Data Analysis

Fundamental Statistical Analysis. For readers not familiar with statistical methods and experienced in the rationale of their use, Motulsky (1995) offers an excellent and basic overview; Chatfield (1988) is advanced but insightful; Abramson (1994), although oriented to epidemiological and clinical studies, presents information for statistical interpretation in an easy-to-read format; and Huff (1954) is mandatory reading for all researchers, managers, and consumers. Good introductory texts in statistics are Campbell (1989), Weinberg and Goldberg (1990), Freund and Wilson (1993), and Zolman (1993). Li (1964) provides an excellent introduction, especially valuable in analysis of variance (ANOVA) fundamentals, but is no longer in print.

The basic fundamental texts for statistical analyses that are used in the classroom as well as by field biologists and ecologists are Box et al. (1978), Steel and Torrie (1980), Zar (1984), Snedecor and Cochran (1989), and Sokal and Rohlf (1994). Arminger et al. (1995) is an advanced text that offers more comprehensive coverage of specialized topics in statistical analysis: missing data, mean- and covariance-structure models, contingency table analysis, latent class models, analysis of qualitative data, analysis of event histories, and random coefficient models. Potvin and Travis (1993) present a summary of references for statistical methods in twelve topic categories: a posteriori testing, density dependence, experimental design, maximum likelihood, multivariate analysis, philosophical issues, ratios, regression analysis, repeated measures analysis, spatial heterogeneity, species associations, and trend analysis.

Parametric Statistics. Parametric statistics represent the well-known statistical methods taught in introductory statistics courses (see references above) and cover the familiar topics of linear regression, ANOVA, and analysis of covariance (ANCOVA). The latter is ANOVA with the addition of a covariate, making it also a linear regression model. A good example of the use of ANCOVA is testing the hypothesis that two salamander populations possess different clutch sizes (an ANOVA model), while simultaneously taking into account that clutch size is a function of body size (a linear regression model). In actuality, linear regression belongs to the family of generalized linear models (GLM), and ANOVA and ANCOVA are special cases of linear regression. Nonlinear, or polynomial, regression and multiple regression (more than one independent or predictor variables) are extensions of the basic model. Fundamentals of GLM and modeling are provided by McCullagh and Nelder (1983), Cullen (1985), Neter et al. (1985), and Dobson (1990). Although regression analysis is well covered in the fundamental texts referenced above, other valuable texts include Draper and Smith (1981), Montgomery and Peck (1982), Neter et al. (1985), and Chatterjee and Price (1991). ANOVA is covered in all basic statistics texts, and an advanced treatise is Searle et al. (1992).

Other regression analyses that have extensive applications in ecology are logistic regression and locally weighed scatterplot smoothing (LOWESS) regression (Trexler and Travis 1993). Logistic regression deals with dichotomous (bivariate) or polychotomous dependent variables and transforms the data to model binomial or multinomial distributions. LOWESS models the relationship between a dependent (response) variable and independent variables under the assumption that neighborhood values of independent variables within a range are good indicators of the dependent variable in that same range.

In traditional least-squares regression, estimators are unbiased (i.e., the expected value is the population parameter). When independent variables are highly correlated (common in ecological data), unbiased estimators produce large variances. Ridge regression has been suggested as a model to obtain biased estimators of regression coefficients and to stabilize variance (Hoerl and Kennard 1970a,b; Montgomery and Peck 1982).

Parametric statistics are based on three important assumptions: (1) population samples or observations are normally distributed; (2) populations (comparisons) possess homogeneous variances (residuals); and (3) observations are independent of one another, that is, that random observations and sampling or experimental errors are independent, therefore avoiding sampling or experimental bias.

These assumptions can be tested formally, but typically they are not. Goodness-of-fit tests and calculations of skewness and kurtosis (available in all basic statistical packages) can test for normality. Bartlett's test assesses homoscedasticity, but its practical value has been questioned (Harris 1975). Sampling independence may be difficult to assess but in some cases can be detected by correlational tests or by the examination of scatterplots of the raw data. In some situations, spatial autocorrelation may present problems for collecting independent samples (see Legendre 1993). Parametric statistical methods are generally considered to be robust with respect to these assumptions when sample sizes are reasonable (e.g., twenty to thirty) and particularly when the raw data have been transformed. A major reliance on robustness is the central limit theorem, which states that the means of variables from nonnormal (e.g., skewed) distributions are themselves normally distributed. Biological data are often log-normally distributed with the mean and variance highly correlated. Biological count data typically form Poisson distributions, where the mean equals the variance. A log transformation for log-normal data and a square-root transformation for data with Poisson distributions are suggested to meet parametric assumptions (Sokal and Rohlf 1994). Additionally, log transformations of the data are effective at stabilizing heterogeneous variances. Therefore, the most critical parametric assumption remains the independence of errors. The violation of this assumption is common and results in a sampling bias.

Milliken and Johnson (1984, 1989) present practical approaches and methods of data analysis for experimental designs and parametric data that are plagued with the well-known problems associated with field data: failures in assumptions, unbalanced designs, lack of replication, repeated measures, multiple comparisons, outliers, and missing data.

Balanced ANOVAs are required to obtain unambiguous interpretations of interaction effects and overall significance. The term "balanced" means that there are equal observations in each experimental treatment. Balanced designs cannot always be used for the practical collection of ecological field data. Shaw and Mitchell-Olds (1993) review ANOVA for unbalanced designs and provide guidelines for the analysis of fixed effects models.

Nonparametric Statistics. Nonparametric statistics (NPS) are also called distribution-free statistics because they make no assumptions about test statistic distribution, variance heterogeneity, and other behaviors. They also respond well to the analysis of ordinal or categorical data. Many researchers believe that nonparametric methods possess low power in contrast to parametric tests. In reality, the difference is not significant (Hollander and Wolfe 1973; Noether 1987). However, what is not always appreciated is that, like parametric tests, nonparametric tests are also subjected to the same two important limitations and violations of statistical analyses: nonindependence of sampling errors (the need for random sampling) and the loss of statistical power when sample sizes are too small (Box et al. 1978; Stewart-Oaten 1995). The chi-square test is the best known, and the most abused, nonparametric test. The fundamental texts for nonparametric analysis are Siegel (1956), Hollander and Wolfe (1973), and Connover (1980).

Potvin and Roff (1993) emphasize the prevalence of nonnormality in environmental data and present the case that distribution-free robust statistical methods should be more extensively used in ecological research and monitoring. Johnson (1995), Smith (1995), and Stewart-Oaten (1995) challenge their conclusion and do not recommend the widespread or routine use of NPS in ecology. Their argument is based on the following issues:

1. NPS should not be a substitute for insufficient sample sizes, poorly conceived experimental or sampling designs, unbalanced data sets, poor field procedures, or just poor data.
2. NPS also require assumptions, which are usually unappreciated, unknown, ignored, or overlooked.
3. It is important that the investigator using the statistical test make an a priori assessment of the relative importance of Type I and Type II errors. See the sections on Statistical Power and Significance Tests (below).
4. Statistical significance is often confused with biological significance or judgment.

Multivariate Statistics. The statistics discussed above deal with data possessing a single dependent (response) variable. Multivariate statistics deal with data that have multiple dependent and independent variables. Suitable introductions are Pielou (1984), Manly (1986), Digby and Kempton (1987), and James and McCulloch (1990). For additional discussion and references, see the review of multivariate methods in Krzysik (1987; Chpt. 42, this volume). Gifi (1990) presents a comprehensive review of multivariate analysis for categorical data and nonlinear models and includes an interesting example of correspondence analysis, where he analyzes and graphically presents the subject material covered in multivariate analysis books (1957–1978). Principal component analysis (PCA) is a powerful procedure for ordination, data reduction, data transformation, and data standardization (Krzysik 1987). PCA produces newly derived variables from linear combinations of the original variables (often highly correlated), such that most of the original variance in the original data is expressed in as few as possible new uncorrelated variables. The use of PCA for ordination has been criticized (e.g., Gauch 1982), but also see the review by Wartenberg et al. (1987).

Nontraditional Statistics. Resampling statistics and permutation/randomization tests represent a rapidly developing field of nontraditional statistics. These are computer intensive procedures that include Monte Carlo methods, the calculation of exact p-values (parametric and nonparametric), jackknifing, bootstrapping (Miller 1974; Efron 1982; Edgington 1987; Noreen 1989; Efron and Tibshirani 1991; Manly 1991; Shao and Tu 1995; Weerahandi 1995), and multiple comparisons (Westfall and Young 1993). These techniques are particularly useful for nonparametric data (appreciable violation of parametric assumptions) and messy data: small samples, unbalanced data (dramatic differences in interpopulation sample sizes), strongly skewed data or residuals, data possessing strange distributions, missing observations, and outliers. Nonparametric tests are desirable because they make no assumptions about the distribution of test statistics. However, like parametric tests, they still rely on asymptotic behavior, which requires reasonable sample sizes and balanced data. Asymptotic theory is not valid for data sets that are small, highly skewed, sparse, or unbalanced. "The difficulty of exact calculations coupled with the availability of normal approximations leads to the almost automatic computation of asymptotic distributions and moments for discrete random variables. . . . How does one justify them? . . . Rigorous answers to [this] question require some of the deepest results in mathematical probability theory" (Bishop et al. 1975). These limitations have been recognized for some time, and Fisher (1935) has suggested the use of permutational p-values for randomized experiments. However, the routine use of permutation methods depends directly on the availability of inexpensive, high-powered computers. Indeed, it is now possible to compute exact permutated p-values for nonparametric tests and thus avoid asymptotic assumptions (Mehta et al. 1988; Agresti et al. 1990; Good 1994).

Jackknifing and bootstrapping are often used to estimate the precision (especially standard error) of descriptive statistics, complicated functions, environmental parameters, and ecological indices. In the jackknife procedure, the original sample data are divided into groups. Usually each group represents a single datum (e.g., a sample with thirty observations would have thirty groups). New samples are generated by deleting each group in turn, one at a time, for the entire original sample. In the above example, there would be thirty new samples, each with twenty-nine observations. The desired statistic (e.g., mean) is calculated from the newly generated samples, and the variability among the samples is used to estimate the standard error of the statistic.

The jackknife procedure reduces bias in the estimated statistic. For a nonnormal distribution, the jackknife is more suitable than the more commonly used F-test (Arvesen and Schmitz 1970).

In the bootstrap, a large number of new sample data sets (usually 1,000 to 50,000) are created from the original data by randomly resampling with replacement from the original data set. For example, let the original data set contain ten observations. Each newly derived data set with its ten observations is generated as follows. The first observation is selected at random from the original data and is "replaced" back into the data set. This process is repeated to select the second observation and is continued until ten observations are obtained. Therefore, for this first resampled data set, a specific observation in the original data may have been selected once, twice, three times, or up to ten times, or it may not be selected at all. This procedure is repeated until the desired number of resampled data sets has been generated. Bootstrapping is a very computer intensive procedure and has only become feasible with the widespread availability of powerful microcomputers. I have run simple algorithms with small data sets (sample sizes ten to thirty) to create 50,000 bootstrapped samples in less than twenty seconds on a 486 PC running at fifty megahertz. Although the bootstrap is much more computer intensive than the jackknife, it is generally considered to be an improvement over the jackknife. Bootstrap and jackknife estimates approach each other asymptotically when sample sizes are large (Efron and Gong 1983).

Reviews of ecological indices are presented in Ludwig and Reynolds (1988), Krebs (1989), and Dixon (1994; see also Krzysik, Chpt. 42, this volume). A practical application of combining several of these techniques for statistical inference in population monitoring can be found in Krzysik (1997).

Analyses of data that are not continuous variables, but represent discrete categories, have become more common with the development of high-power microcomputers and associated statistical software. Important literature in this field includes Cox (1970), Bishop et al. (1975), Everitt (1977), Fienberg (1980), Plackett (1981), Fingleton (1984), Young (1987), Agresti (1990), Gifi (1990), and Nishisato (1994).

Meta-analysis is an important statistical procedure for analyzing as a group the combined results of individual experiments (Cooper and Hedges 1993; Petitti 1994). Its utility is two-fold: (1) none of the individual experiments or studies may have sufficient statistical power to adequately test the significance of the hypothesis posed; and (2) it provides a mechanism to produce generalizable results from possibly very specific experiments. Meta-analysis is a new technique in ecological research (Gurevitch et al. 1992; Gurevitch and Hedges 1993) but has had a strong foundation in medicine and social studies, fields where sample sizes tend to be low, inherent variability tends to be high, manipulative experiments are out of the question or unethical, and data are expensive. Meta-analysis was successfully used by the U.S. Environmental Protection Agency (1990) to assess and verify the risk of lung cancer to women exposed to environmental tobacco smoke. Meta-analysis consists of using the statistical engine to take the data of independent experiments, combine them, and reach valid generalized conclusions.

Another nontraditional approach is Bayesian inference. Although Bayes's theorem was published in 1763, its acceptance and rejection vacillated since that time (Box and Tiao 1973). It is currently increasing in popularity. The strength of the Bayesian approach is that it is based on, and takes full advantage of, incorporating prior information (e.g., previous data or experiments) into a current statistical analysis (Box and Tiao 1973; Lee 1989; Press 1989).

Time series analysis is relevant in many biological, ecological, and environmental applications, representing the measurement and analysis of parameters as a function of continuous or discrete time (Chatfield 1989; Diggle 1990; Brockwell and Davis 1991; Rasmussen et al. 1993).

Data measured as angles, or two- or three-dimensional orientations, are common in the sciences, including biology and in any spatial applications. Important applications in biology would be the design and analysis of experiments in homing; movement of animals from point of release; directional movements of animals in response to external stimuli such as noise, ground vibrations, wind, ocean currents, wildfire, flooding regimes, circadian rhythms, physical or chemical impacts, and habitat manipulations. These data are known as circular, or spherical, data and require specialized statistical analysis with appropriate models (Fisher et al. 1987; Fisher 1993).

Efficient Statistical Inference

Type I (α) and Type II (β) Errors. Every basic text in statistics discusses Type I and Type II errors. A Type I error is the probability of rejecting a true null hypothesis (no significant difference). Selecting a smaller value of α reduces Type I error (e.g., select an α of 0.01 instead of 0.05). α is also known as the p-value and represents the probability of selecting random samples that result in a significant p-value (α) when the difference between group means is Δ.

A Type II error is the probability of failing to reject a false null hypothesis. It is important to note that the correct phrase is "failing to reject" rather than "accepting" a null hypothesis, because a failure to disprove a given null hypothesis does not prove it. Indeed, if I found no "significance difference" and sample sizes were small and/or inherent variability was high, it would be incorrect to state that I "proved" the null hypothesis, when in fact it is more correct to say I failed to reject the null hypothesis, possibly because statistical power was low.

Conservative Analysis. A conservative statistical analysis strategy guards against making a Type I error. A conservative strategy includes the a priori selection of conservative statistical tests or the selection of low α values.

Statistical Power. The power of a statistical test is defined by $1 - \beta$. Therefore, power is the probability of rejecting a false null hypothesis. In other words, high power is directly related to a smaller β (a lower Type II error). β represents the probability of selecting random samples that result in a nonsignificant p-value (α) when the difference between population means is Δ. Both α and Δ must be selected a priori and are independent of statistical intervention. Both are dependent on the technical experience or judgment of the investigator in selecting what the difference between population means should be before it is considered statistically significant under the null hypothesis, with the probability α of making a Type I error. Power represents the probability of obtaining a significant difference when the difference between population means is Δ. The power of an analysis is therefore related to inherent variability, sample size, and the difference between population means (Δ) that I want to call a statistically significant (α) difference.

Statistical power analysis should be conducted as an integral component of the experimental design before a study is implemented and should also be reported in the published results of the study. This applies to both research and environmental management projects. The standard text for power analysis is Cohen (1988), and software to conduct the analysis is available (Borenstein and Cohen 1988).

Statistical results that are reported to have low power, or appear to have low power when no power analysis was reported, should be looked at with skepticism when conclusions are reached that are based on the failure to reject a null hypothesis—the failure to find significance. Peterman (1990a) found that 98 percent of recently surveyed papers in fisheries and aquatic sciences that did not reject a null hypothesis failed to report statistical power or β. Additionally, 52 percent of these papers reached conclusions as if their null hypothesis were true. Peterman (1990a) presents an important fundamental discussion of power analysis in statistical inference and of its implications for researchers, policy makers, and decision makers in environmental management. Peterman (1990b) also draws attention to the absence of power analysis in assessing the effects of acidic deposition on forest declines. These papers should be required reading for researchers and resource managers contemplating the design of any large-scale ecological or environmental monitoring programs. The high inherent variability of natural systems presents a formidable obstacle to designing environmental monitoring programs with sufficient power to detect changes or trends (Pechmann et al. 1991; Osenberg et al. 1994). Additional suggested readings include Tacha et al. (1982), Toft and Shea (1983), de la Mare (1984), Rotenberry and Wiens (1985), Swihart and Slade (1986), Gerrodette (1987), and Green (1989). See also the section on Significance Tests (below).

Increasing Statistical Power. There are several ways to increase statistical power. First, use large or at least appropriate sample sizes, which increases degrees of freedom. Increasing sample size is the most important and usually the most feasible way of increasing power.

Second, design experiments that have small error variance (within population variance) and reduced confounding effects. This produces a smaller denominator in the F-test, and therefore significance can be detected with smaller between treatment variance.

Third, increase the value of α. This is the usual alternative when sample size cannot be increased. Although this increases power and reduces the chances of making a Type II error, it increases the chances of making a Type I error. There is a mutual trade-off when selecting between making a Type I or a Type II error (you cannot have your cake and eat it too).

Fourth, increasing Δ increases power, because at any level of sampling variability, it is more reassuring to attribute significance to larger differences than to smaller differences.

Finally, report a power analysis with your data. Based on your sample size and the inherent variability in your data (error variance), how small a difference could you have detected as significant with the α value that you a priori selected?

Robustness. Large sample sizes create high degrees of freedom. No matter how complicated an ANOVA, the degrees of freedom in the denominator for the F-test are the most important factor for judging significance.

There are two additional important factors to consider. Statistical comparisons (populations compared) should be similar in sample sizes, and two-tailed tests are more robust than one-tailed tests.

Harris (1975) concludes that most data sets in univariate, parametric-based statistical tests are robust to the assumptions of normality and homogeneity of variances, unless sample sizes are small and unequal. Harris (1975) suggests the following guidelines:

$$Var_{max}/Var_{min} < 20 \quad (Var = \text{sample variance})$$

$$N_{max}/N_{min} < 4 \quad (N = \text{sample size})$$

$$\text{Error degrees of freedom} > 10$$

Significance Tests. There is a great deal of empirical evidence (Morrison and Henkel 1970; Roberts 1976; Guttman 1985; Gardner and Altman 1986; Jones and Matloff 1986; Oakes 1986; Perry 1986; Millard 1987; Krebs 1989; Wiens 1989; Yoccoz 1991; McBride et al. 1993; Motulsky 1995) and historical consensus from statisticians (Tukey 1960, 1980, 1991; Wolfowitz 1967; Deming 1975; Pratt 1976; Cox 1977, 1986; Carver 1978) that significance tests have been excessively used and misapplied, particularly in regard to confusion with biological significance or relevance (see also the preceding subsection on Increasing Statistical Power). Statistical practitioners have dismissed the cautions of statisticians for over a half century (Berkson 1942). Salsburg (1985) refers to hypothesis testing as the primary tool in the religion of statistics. There is no empirical or theoretical foundation for selecting $p = 0.05$, as is routinely done in biological data analysis and tests for significance. P-values cannot even be compared among studies, because they are a function of specific project design parameters and sample size (Gibbon and Pratt 1975). In a demonstration of the applicability of significance tests to contrast soil pH among fields and to evaluate United States regulations for groundwater quality, McBride et al. (1993) conclude that significance tests have no practical value or merit and recommend that researchers and environmental managers place more value on statistical power and deciding on "practical differences" when statistical comparisons are being made among means and their variances.

There is an important difference between biological/ecological and statistical significance, although this is often overlooked. Biological/ecological significance represents biological realism and common sense directly relevant to actual ecological systems. Statistical significance is only relevant to sample size in the specific context of the probability of finding an observed difference by chance alone, relative to the inherent variability in the system under investigation. Biological relevance does not enter into the equation. Statistical significance will always be assured as long as sample size is large enough to "statistically detect" even the smallest differences, differences that are undoubtedly irrelevant to the normal course of biological variability. Therefore, a statistical significance is not necessarily of practical or relevant significance. At the other end of the spectrum, sample sizes that are too small relative to the inherent variability of ecological systems (low statistical power) may fail to find biological relevance when it is present. The testing of significance for multiple comparisons is not valid unless equal sample sizes are used.

Although most statisticians and researchers who apply statistics to their experiments do not advocate the abandonment of significance tests, there probably is consensus that more care should be taken in their use. It is more desirable to present means with their standard deviations (standard errors) or confidence intervals and sample sizes (Cochran and Cox 1957; Gardner and Altman 1986; McBride et al. 1993).

Transformations. Probably the most common source of sample heterogeneity in biological data is that the mean and variance are correlated. Data transformation (especially the log transformation)

$$X_T = \ln (x+1)$$

(X_T is the transformed variable x, and ln is the natural logarithm)

removes the functional dependence of the mean and variance. Log transformation is also effective in stabilizing unknown sources of heterogeneity, as long as they are not too extreme. Steel and Torrie (1980) refer to this as irregular error heterogeneity. The source of this heterogeneity could be due to outliers, spatial heterogeneity, or procedural errors. Outliers may represent natural variability (possibly indicating small sample sizes) or important departures from the data, and their removal should be considered cautiously (see Barnett and Lewis [1984] for guidance). Outliers could also be due to procedural errors, which are beyond statistical treatment, and in this case they can be removed. Spatial heterogeneity is best handled by sample stratification, but this is difficult or unmanageable if the spatial pattern is not obvious. Inherent spatial complexity and mosaics, especially at scales much smaller than the sampling area of interest, are best handled by nested sampling designs.

The most commonly used transformations are the log and square root (e.g., Sokal and Rohlf 1994). The log transformation is most frequently used because it possesses many desirable properties, including making variables independent of scale (Jolicoeur 1963a,b; Marriott 1974). Scale independence is a critical consideration, especially in multivariate analysis, otherwise the results of the analysis may depend on the scale of the original measurements (Gower 1967; Orloci 1967; Noy-Meir et al. 1975; Pimentel 1979). The square root transformation is most commonly used in count data, which typically follow a Poisson distribution (mean and variance are equal). Guidance and practical references for data transformations are Elliott (1977), Green (1979), Steel and Torrie (1980), Draper and Smith (1981), Zar (1984), Snedecor and Cochran (1989), Fry (1993), and Sokal and Rohlf (1994).

A broad family of transformations can be derived from modeling power series (Healy and Taylor 1962; Box and Cox 1964; Draper and Smith 1981; McCullagh and Nelder 1983). Southwood (1966) discusses the use of Taylor's power law. Southwood (1966), Poole (1974), Elliott (1977), and Green (1979) discuss the fitting of negative binomial distributions. Williams and Stephenson (1973) discuss cube-root transformations.

Transformations can also include methods that rank, standardize, or statistically manipulate raw data into a "new data set." Green (1979) recommends transforming the raw data to ranks and then using Fisher and Yates tables (a comprehensive set of statistical tables published in 1974) to transform to standardized deviates, making rank values independent of sample size.

An important transformation for multivariate data is the use of principal component analysis (PCA; Krzysik 1987). Significance tests in multivariate analysis, as in parametric analysis, assume independence in independent (predictor) variables. A PCA transformation before multivariate analysis of variance (MANOVA), discriminant analysis, and multiple regression would produce the desired criteria of independence. Green (1979) emphasizes that the assumption of independence is the one most frequently ignored in statistical analysis. Another important advantage of PCA, and using a correlation matrix of original variables as input for the PCA analysis, is that scale magnitude (including logarithmic variables such as pH), and even the mixing of all possible numerical scale variable types (ratio, interval, ordinal or rank, bivariate), is completely and efficiently standardized (mean of zero and unit variance; Krzysik 1987). Nominal scales other than bivariate ones may or may not be combined validly with continuous and rank data. See Hayek (1994) for a description of numerical scales.

Issues in Experimental Design

Experimental Design

The foundations of experimental design were developed by Fisher (1935) for manipulative laboratory (genetic) and agriculture field experiments. Since the classic references in experimental design were first published by Cochran and Cox (1957) and Cox (1958), there was for a time a conspicuous absence of texts in this field. (Both of these texts, Box and Tiao (1973), and others were reprinted in 1992 in the John Wiley and Sons Classics Library Editions.) Treatments of experimental design by standard statistics texts are usually limited to the design of ANOVA comparisons (e.g., factorial, nested, split-plot, Latin square). Lindman (1992) presents a comprehensive treatment of ANOVA in experimental design. With the realization of a vacant niche, a surge of experimental design texts were published in the late 1980s and early 1990s. Selected examples include Kish (1987), Mead (1988), Keppel and Zedeck (1989), Montgomery (1991), Atkinson and Donev (1992), and Manly (1992). In the interim, a Canadian aquatic ecologist published a synthesis of experimental design and data analysis that has been relevant for practicing field biologists and ecologists (Green 1979). Despite its age, the applicability of Green's text remains current, and it is still in print. In this discipline, the publishing date has little bearing on the contemporary applicability. Fisher's (1935) tool box contains the fundamental basics of statistical and design tools, and even at this early stage in the development of experimental design Fisher realized the value of permutation/randomization tests. However, it was only the advent of high-speed microcomputers that made these tests feasible and routine (see the subsection on Nontraditional Statistics, above).

Additional practical discussions of experimental design for field biologists include Milliken and Johnson (1984), Hairston (1989), Skalski and Robson (1992), and Hayek (1994). Two books, Fry (1993) and Scheiner and Gurevitch (1993), address a remarkable range of statistical design and analysis issues in the context of real examples of current research interest and high relevancy to biology and field ecology.

The need for valid experimental designs for environmental monitoring has been emphasized (Leibetrau 1979; Hurlbert 1984; Millard and Lettenmaier 1986; Stewart-Oaten et al. 1986; Legendre et al. 1989; Keith 1990; Eberhardt and Thomas 1991; Rose and Smith 1992; Underwood 1994). Because water quality is of major public concern and represents important issues in environmental policy and politics, experimental designs and sampling protocols for aquatic ecosystems have attracted much more attention than have those for terrestrial landscapes (Montgomery and Hart 1974; Leibetrau 1979; Loftis and Ward 1980; Casey et al. 1983; Hirsch and Slack 1984; Ward and Loftis 1986; Ward et al. 1986, 1990; Perry et al. 1987; Sanders et al. 1987; Hirsch 1988; Taylor and Loftis 1989). Advancements made in the monitoring of water quality include the statistical treatment of data at or below detection limits (Gleit 1985; Porter et al. 1988; Helsel 1990).

Eberhardt (1976), Hurlbert (1984), Eberhardt and Thomas (1991), and Underwood (1991, 1992, 1994) have reviewed the issues and brought renewed attention to the difficulties of achieving true replication in ecological experiments and environmental field settings. The problems encountered in meeting the assumptions and challenges of experimental design principles have been recognized for some time by researchers outside of laboratory settings (Campbell 1957; Stanley 1961; Campbell and Stanley 1963; Cook and Campbell 1979). Campbell and his colleagues refer to environmental and social experiments as quasi-experimental designs. Milliken and Johnson (1989) provide a discussion and practical guidance for the analysis of unreplicated experiments. All the references in this paragraph should be required reading for serious field biologists.

Experimental design has been routinely applied to ecological field studies for both manipulative and mensurative experiments (Hurlbert 1984). Mensurative experiments are defined by Hurlbert (1984) as involving the making of measurements at one or more points in space or time. Space or time is the only experimental treatment. There is no imposition or manipulation of external factors on the experimental units to constitute a treatment. "The defining feature of a manipulative experiment is that the different experimental units receive different treatments and that the assignment of treatments to experimental units is or can be randomized." If true randomization of experimental treatments by manipulative assignment cannot be achieved, then replicates are not independent. Hurlbert called this pseudoreplication, and the testing of treatment effects occurs with an error term inappropriate to the hypothesis being considered. The validity of using unreplicated treatments rests on the tenuous assumption that all experimental units are identical at the start of the experiment or manipulation and that they remain identical (with respect to the treatment) throughout the experiment. Therefore, it follows that the experimenter would not know if the finding or not finding of significance was due to treatment effects or some unknown factor related to the experimental plots not being identical. Hairston (1989) also reviews and discusses issues of ecological field experiments and the potential problems involved.

Pseudoreplication. Pseudoreplication can arise in a variety of ways (Hurlbert 1984), and it is worthwhile for field biologists to review the concept.

1. Replicates are not independent
   a. treatments are spatially or temporally segregated
   b. treatments are correlated, interconnected, or somehow related
   c. "replicates" are samples from a single experimental unit (i.e., subsamples)
2. Nonindependent (nonrandom) assignment of treatments
3. Lack of interspersion
4. Sequential samples for each experimental unit are taken over each of several days
5. Dates are considered replicates of treatments
6. True replicates are pooled prior to analysis
   a. an unfortunate loss of information on the variance among treatment replicates
   b. reduces degrees of freedom and power of analysis
7. Combining variance *among* replicates with variance *within* replicates (subsamples) produces confounding and unknown effects

Components of an Experimental Design. There are four considerations in an experimental design: controls/treatments, randomization, replication, and interspersion.

The terminology of controls can be used in a variety of ways. A control is any treatment against which one or more treatments is compared (Hurlbert 1984).

1. Receives no treatment. This is the familiar identification of a "control."

2. A before-treatment control can also be used as the experimental unit before a treatment is imposed.

3. Regulation of experimental conditions. Controls may refer to the establishment of homogeneous experimental units, the precision of treatment procedures, or the regulation of the physical or chemical environment.

4. A procedural effect control is used to evaluate the effects of a procedure that accompanies a treatment but whose effects are not under investigation or to eliminate confounding effects. Needle injection and the psychological control of placebos are common examples.

5. Temporal change controls are used to monitor potential temporal changes to experimental units.

6. Experimental design features can be used as controls to minimize the effects of sources of confusion in experiments and include randomization, replication, and interspersion (Hurlbert 1984).

Randomization ensures that errors are independent and normally distributed. This guards against experimenter bias and systematic and correlated errors and ensures knowledge of α (the p-value that is necessary for determining significance).

Replication controls for stochastic factors (random error) that are introduced by experimenter-generated variability, inherent or initial variability among experimental units, or chance events affecting an experiment in progress.

Interspersion controls for known or unknown spatial variation due to spatial heterogeneity or environmental gradients for either initial conditions or chance events affecting an experiment in progress. Interspersion also controls for experimenter bias and assures statistical independence.

BA/CI Experimental Designs

Before and after/control and impact (BA/CI) experimental designs address the pseudoreplication issue in environmental or ecological field experiments and were originally discussed by Green (1979). BA/CI designs involve taking samples before the impact (e.g., effluent discharge) begins and after it takes place at both control and impact sites. Sampling is replicated in time. In 1979 I designed a study to test habitat selection parameters in neotropical migrant birds in southern Illinois oak-hickory upland forests. The design was to test the null hypothesis that subcanopy or small understory trees do not affect nest site selection in these species. The study was to take place on lands purchased or leased by a coal company for strip-mining. Six large similar tracts of forest lands were available. Four 20-hectare study plots were placed in the central portion of four forest tracts (randomly determined). The four plots were randomly assigned as two control and two treatment plots. The treatment consisted of the removal of subcanopy trees. The study was designed such that birds would be surveyed for two breeding seasons in all four plots before treatment. The trees would be cut in the two treatment plots in the fall following the second survey season. The breeding bird surveys would continue for two more years in all four plots. Differences between control and treatment could be compared as variance components with time as a "replicate." Funding cuts, however, prevented the implementation of the project.

Stewart-Oaten et al. (1986) designed a similar study to assess experimentally the effects of point source effluent discharge into aquatic ecosystems, but their design had only one control-treatment contrast. The authors review the concept and applicability of BA/CI and provide a rich source of references. A similar BA/CI design was used to assess the effects of nuclear reactor coolant effluent on kelp forests off the coast of southern California (Schroeter et al. 1993). Osenberg et al. (1994) and Thrush et al. (1994) further discuss the BA/CI concept in environmental monitoring.

Underwood (1994) has reviewed and rejected the BA/CI design whenever it has a single control location and therefore no spatial assessment of variance components. Underwood (1994) recommends asymmetrical designs where several control locations are used to assess a given treatment effect. In this way, not only can environmental impacts or changes be assessed in the traditional fashion (e.g., trends in mean population density) but, additionally, impacts that alter temporal variance can be detected, because temporal interaction terms can be statistically tested.

Sampling Design

Technical guidance for sampling is available (Cochran 1977; Elliott 1977; Williams 1978; Desu and Raghavarao 1990; Thompson 1992). An excellent introduction that should be read by all field biologists is Stuart (1984). Nested quadrat designs are typically used to determine the most efficient size of the primary sample unit (Greig-Smith 1964; Kent and Coker 1992). Sample unit size makes no difference in the case of randomly distributed organisms, while with clumped organisms, smaller sample unit size results in estimates with increased precision.

The importance of large sample sizes is that statistical analyses are robust to violations of assumptions when they are based on a large number of error degrees of freedom. There are two reasons for this. Sample means from even nonnormal and heavily skewed distributions approach normal distributions as sample size increases, a consequence of the central limit theorem. The F-statistic, which determines statistical significance, increases as error degrees of freedom increase, and as a result significance can be determined with smaller differences between (among) population means. For all practical purposes, sample size and not the fraction of the population sampled determines the precision of an estimate. In a well-designed sampling and statistical design, three replicates per treatment combination are generally sufficient. An easily derived expression for estimating required sample size is found in (Eckblad 1991):

$$\text{Sample size} \sim (t_\alpha)(\text{var})/(\text{acc x mean})^2$$

where t = t-value from t-table at the desired α level, var = sample variance, acc = accuracy as desired proportion from the true mean, and mean = sample mean.

King (1980, 1981) provides a good introduction and practical guidance for sampling strategies based on statistical distributions and probability charts. The statistical distributions covered are uniform, normal, lognormal, binomial, chi-square, Weibull, gamma, extreme value, logarithmic extreme value, reciprocal functions, and hazard rate functions.

Ecological Design

The statistical rigor of Hurlbert's (1984) conclusions are undeniable. However, in practical field evaluations of treatment-control effects and using common sense, it is routinely observed that treatment-effect differences are much greater than potential effects relevant to inherent differences in experimental plots.

The term "ecological design" is more appropriate and is recommended as a less ambiguous replacement for the following terminology—experimental design, quasi-experimental design, sampling design, or research design—when used in the context of ecological field experiments or ecological/environmental assessment and monitoring protocols. Ecological design would include field designs that are "true" manipulative experimental designs, unreplicated experiments, sampling protocols, and the field design issues addressed by Eberhardt and Thomas (1991).

Basic Principles of Ecological Design and Analysis

Green (1979) introduces ten principles of research design and analysis that merit discussion.

1. Clearly and completely communicate to your audience or readers the objectives of your study, the statement of your hypothesis, and the formulation of your ecological design, sampling strategy, field methods, and statistical analyses procedures. These concepts must be tightly integrated throughout the entire project. For example, it is invalid to change objectives or hypotheses partway into a project, because the experimental or sampling design may no longer be applicable. Despite the logic, intuition, and necessity of this approach, these fundamentals are commonly violated (Rose and Smith 1992). Once the objectives and approach of your study have been determined, it is advised to seek peer review or design/analysis expertise.

2. Sample replication is required for each combination of treatment-control comparisons or any other controlled variable. Differences between spatial and/or temporal comparisons (and their interactions) can only be determined by comparisons of variability between treatments and controls to variability within treatments and controls. This is the basis of the F-statistic (in ANOVA) or some multivariate analog of it.

3. An equal number of random replicate samples should be taken for each combination of controlled variables (treatments-control). Sampling in "convenient," "representative," or "typical" locations is not random sampling. Random sampling ensures independence of sampling errors, an important assumption of statistical inference. Glass et al. (1972) demonstrate that correlated errors represent the most serious violation to the validity of significance tests.

Most statistical analyses can be conducted with unequal sample sizes, and typical examples include one-way ANOVA and linear regression. Complex ANOVA designs without equal sample sizes can also be easily analyzed with modern computer statistical packages because the complex algorithms and calculations required remain transparent to the user. However, in complex ANOVA, especially factorial designs, equal sample sizes are required for unambiguous interpretation of interaction components of variance and overall effects.

4. To test if a condition or treatment has an effect, sampling must be conducted where the condition is present and where the condition is absent, while everything else is the same. An effect or treatment can only be demonstrated by statistical comparison with a control.

Although this principle is obvious in theory and forms the basis of experimental design, it is controversial in applications of typical field studies (e.g., see Hurlbert 1984).

5. A pilot study is well worth the time and resources invested. Preliminary sampling provides a basis for evaluating sample sizes, statistical power, parameters of sampling design, statistical analysis options, and the logistics and fine-tuning of field methods.

6. Verify if sampling design has adequate and equal efficiency over the entire range of sampling conditions encountered. If there is a variation or bias in the spatial, temporal, or population representativeness you are sampling, treatment comparisons are biased and invalid. For example, suppose you are interested in comparing acorn production by white oaks as a function of canopy closure. Because open forest canopies possess denser ground cover vegetation, one has to ensure that the sampling efficiency of acorns on the ground is independent of ground cover. A temporal example would be an interest in seeing if fish abundance and diversity changed with time in a specific stretch of stream. If a different mesh size in the seine was used on two different occasions, the temporal comparisons are invalid. Similarly, if electroshocking was used on two different occasions when the conductivity of the water was different, temporal comparisons are biased. Animals that become "trap-happy" or "trap-shy" alter the representation of the population being sampled.

7. Stratify sampling in heterogeneous environments. This is also known as blocking in an experimental design. Spatial heterogeneity is typical in all field situations involving ecological experiments, and the experimental design should accommodate this reality (see Dutilleul 1993; Thrush et al. 1994). If a given area to be sampled has a large-scale environmental pattern, the area should be classified into subareas or plots (stratas) that form more homogeneous units. Strata should be constructed such that within-strata variances are minimized while between-strata variances are maximized. The sampling effort should be allocated in proportion to the area of each of the identified plots. The main purpose of stratifying is to increase statistical power by controlling for variance between subplots—reducing within-plot variance and therefore the denominator in the F-statistic.

When it is suspected that sources of variation are hierarchical or on very small scales, nested or subsampling designs are most appropriate.

8. Verify that the size of the sample unit is appropriate to the size, density, and spatial distribution of the organism that is being sampled. Estimate the number of replicates required to obtain a desired level of precision. An important fact of reality is that logistic and economic considerations often determine the size and number of sampling units. As a general rule, fewer large samples are cheaper and/or easier to collect than many small ones. However, from the perspective of sampling theory, many small samples are usually statistically more valid than a few large ones. An important consideration is that results of statistical analyses should be independent of sample size.

9. Test data for adherence to statistical assumptions. Data should be tested to determine if error variation is normally distributed, homogeneous, and independent of the mean. In the case of most field data, these assumptions do not hold, but for practical purposes parametric inference is robust (see subsection on Robustness, above). A number of options are available to the investigator: appropriate data transformation, use nonparametric statistics, use resampling statistics, use an appropriate sequential sampling design, and test against simulated null hypothesis data.

Testing serious deviations from assumptions belongs in the realm of exploratory data analysis. Scatterplots or histograms of raw data, error terms (residuals), and sample variances and covariances provide the best insight into variance heterogeneity. Bartlett's test may be too sensitive to be of practical value (Harris 1975). Sokal and Rohlf (1994) recommend treating the ratio of the largest to the smallest sample variance as an F-statistic and an alternative to Bartlett's test.

Heterogeneity of error variances decreases the power of the analysis, resulting in a higher probability of a Type II error (Cochran 1947). When groups with the larger variances have larger sample sizes, the statistical test employed is more conservative (i.e., the p-value, or α, is in reality smaller than believed; Glass et al. 1972). On the other hand, when groups with the larger variances have smaller sample sizes, the test is more liberal (p-value, or α, is effectively larger).

10. Having chosen the best statistical methods to test your hypothesis, stick with the results of your analyses. It is incorrect and not statistical inference to select a posteriori statistical methods or significance levels to "statistically verify" what you wish your data to demonstrate.

Common Problems in Ecological Design and Analysis

The following is summarized from experience and the references used in this chapter. Green (1979) and Fowler (1990) also provide reviews of the common problems encountered in statistical analyses.

1. Procedural errors almost always have more detrimental effects to the valid outcome of a project than experimental or statistical (sampling, measurement) errors (Lessler and Kalsbeek 1992). This is why a good, efficient sampling design is usually more effective than excessive sample sizes and even 100 percent sampling. Sampling intensity generally increases the occurrence of procedural errors. Procedural errors are those caused by carelessness, sloppy or inappropriate field methods, poor or inappropriate sampling design, lack of a quality assurance and control program, inexperience, fatigue, and mistakes in data collection or recording. Statistical analysis usually cannot control, or make adjustments for, procedural errors.

2. Assumption of independence among independent (predictor) variables. This is especially violated in multivariate statistics where there are many independent variables and several to many dependent variables. Environmental variables by their very nature and the interdependencies of ecological systems are usually (often very strongly) correlated.

3. Hypotheses and p-values (α) must be defined a priori. The null hypothesis can never be proved.

4. Random sampling is absolutely necessary to avoid the serious pitfall of biased sampling. If error terms are not independent, systematic or correlated errors may result, and significance tests are invalid. The nonindependence of error terms precludes us from knowing α.

5. A valid experimental design requires replication of all combinations of treatments and controls. This is usually only feasible and practical in laboratory and agricultural settings. True replication in most environmental field studies is difficult or impossible to realize. This problem has been thoroughly reviewed by Eberhardt (1976), Hurlbert (1984), and Eberhardt and Thomas (1991), but see Hawkins (1986). The case for pseudoreplication has probably been overstated on practical grounds, because field experiments to evaluate "effects" are usually designed such that the differences between treatments and controls typically far exceed the inherent or background environmental differences among experimental units and overshadow the "supposed" confounding effects of using pseudoreplicates instead of "true" replicates.

6. When obvious large-scale spatial variability is present, samples should be stratified. When small-scale heterogeneity is known or suspected, a nested sampling design should be used. In both cases the strategy is to reduce within-sample variance components. This reduces the error term in the F-statistic or its multivariate equivalent, effectively increasing the power of the analysis. This increases the validity of significance testing.

7. Avoid doing many separate t-tests. When you analyze all possible pairs of comparisons, you do not know the true value of α. Your alternatives are to use a priori orthogonal contrasts (Sokal and Rohlf 1994) or design a balanced multifactorial ANOVA. The latter design, with as low as three replicates per treatment combination, represents a powerful analysis because error term degrees of freedom are reasonably high and treatment interactions are tested. A less desirable alternative is to decrease the α-value (i.e., force the significance to be more conservative). This entails adjusting α by the Bonferroni procedure (Day and Quinn 1989; Zolman 1993) or the Dunn-Sidák procedure (Sokal and Rohlf 1994). The same problems arise when doing multiple comparisons of linear regressions. Fry (1993) recommends Bonferroni adjustments to calculate confidence intervals for predictions from regression equations.

8. When you have failed to reject your null hypothesis, calculate the power of your statistical design. Actually, a power test should have been conducted a priori as part of your overall experimental/sampling design. The failure to conduct a test for statistical power is potentially a serious concern in studies relevant to conservation biology and endangered species because a statistical assessment or monitoring program with low statistical power could fail to detect population trends or other experimental parameters of interest.

9. A posteriori multiple comparison tests (MCT) should be used with caution (Perry 1986; Tukey 1991). Adjusting α is also important. Follow the advice of Day and Quinn (1989) and Westfall and Young (1993). MCT are also discussed in Fry (1993), Zolman (1993), and Sokal and Rohlf (1994). A major problem with MCT is the use and determination of significance (adjustments to α). MCT should not be conducted when the main effect in an ANOVA is not significant. A priori orthogonal contrasts (Sokal and Rohlf 1994) and two-way ANOVA with interaction term are preferred alternatives to MCT.

10. Repeated measures or observations of the same individual or population are not independent events. Neither are field experiments where observations or data are spatially or otherwise correlated or collected from the same plot. Nonindependence of measures strongly violates parametric assumptions and requires special analysis (Gurevitch and Chester 1986; Crowder and Hand 1990; Roberts 1992).

11. When using statistical tests, particularly multivariate but also parametric ones, be aware of the assumptions the tests make, and test your data to evaluate them. Check raw data for homogeneity of sample variances. Check residuals for normality and independence of errors. The treatment of categorically dependent variables as continuous variables in an analysis is usually not recommended and should be approached with caution.

12. Interpret interaction effects in multiway ANOVAs correctly (Steel and Torrie, 1980; Fry 1993; Sokal and Rohlf 1994). The area times time interaction term in an ANOVA represents pseudoreplication (Hurlbert 1984).

13. Do not pool populations or plots without justification. Although Sokal and Rohlf (1994) provide guidance about when to pool data, it is not a generally recommended practice. Pooling results in the loss of variance estimates and reduces the degrees of freedom for the error term. Pooling also compounds treatment and population (plot) effects.

14. Avoid step-wise techniques (e.g., step-wise regression, step-wise discriminant analysis). Because environmental variables are usually highly correlated, the use of step-wise techniques to extract a ranking of predictor variables may produce spurious results that would not be relevant to any underlying environmental reality.

15. Be aware of confounding effects in your experimental design. Confounding effects of environmental variables are always present because of their high natural intercorrelations, including spatial and temporal relationships. This is the main reason that step-wise techniques should be avoided (Green 1979).

16. Qualitative data or bivariate data may often be equal to, or superior to, quantitative data and much more efficient and economical to collect. Ranked data may be more efficient (economical) to collect and may be superior to continuous data.

17. Do not conduct statistics on ratios. Ratios follow the Cauchy distribution, possess larger variance than either original variable, represent a biased estimate of the mean, and increase size-dependence when attempting to adjust for scale (summarized in Green 1979). Fleiss (1981) is the standard reference for statistical treatment of ratios.

18. The use, and more important the ease of use, of multivariate statistics has dramatically increased with the availability of modern, high-speed microcomputers and user-friendly software packages. The user is often conducting multivariate procedures without any idea of the fundamental mechanics of the analyses, much less the analyses assumptions and applicabilities. Multivariate techniques may be very sensitive (some more than others) to assumptions of multivariate normality, equivalent dispersion of covariance matrices (comparable to univariate homoscedasticity), and intercorrelation of predictor variables. The need for large sample sizes is the rule and rarely the exception, even with careful ecological designs and high-quality data sets. Discriminant analyses in particular are susceptible to widespread abuse and misunderstanding. See James and McCulloch (1990) for an overview of multivariate analysis and the reviews by Williams (1983) and Williams and Titus (1988) for discriminant analysis.

Designing an Ecological Monitoring Program

The design of any ecological or environmental monitoring program, including the monitoring of ecological indicators, specific taxa (e.g., amphibians), or populations (e.g., endangered species), requires a relatively rigid approach or protocol. This is especially important because costs are high, ecological risk may be at stake (e.g., extinction of a species or population), and temporal considerations are important (i.e., an invalid design or field methods or the collection of inappropriate data parameters relative to stated objectives is discovered several years into the program). The following protocol is recommended. The process will be discussed as an ecological or biological project, but the principles apply to any study. A complete protocol will be described, but the details would depend directly on specific objectives and the magnitude of the project. Obviously a global or detailed regional program would be several orders of magnitude more complex and expensive than a local, focused effort.

Scoping. The scoping process entails the gathering of the major players involved in the project, including sponsors, administrators, environmental managers, field biologists, statisticians (design and analysis), computer specialists (database management, programming requirements, GIS requirements), and those with other specialized expertise (e.g., legal, if legal isuues cannot be avoided). This stage also includes the delegation of specific duties whenever partnerships are involved, and Memorandums of Understanding (MOUs) are required. Regional studies are becoming increasingly common for a number of reasons: economics, avoidance of duplication, sharing of expertise and data, magnitude of project, higher chance of success, leveraging of funding opportunities, balancing of environmental-economic-social conflicts, and the need to share responsibilities and legal mandates. Regional approaches would typically include federal, state, and possibly local agencies; private parties, including property owners and conservation groups; and whatever additional technical and legal experts are required (e.g., consultants and academics). The scoping process assists in generating consensus, project purposes and goals, and individual responsibilities and sets the stage for project objectives.

Objectives. Project objectives are arguably the most important component of a monitoring program. It has been my experience that the failure to develop or follow explicit project objectives is the most common reason for the failure of both large- and small-scale monitoring projects. Objectives must be explicitly stated in a written form and are closely associated with the scoping process. Objectives determine project priorities, focus, and specifics.

Scale and Resolution. Scale and resolution are more specifically defined in landscape ecology terminology as extent and grain (see Krzysik, Chpt. 42, this volume). Extent is the largest spatial unit of the project (e.g., the state of Illinois, the Midwest region, or conterminous United States). Grain is the smallest resolvable unit for analysis (e.g., 1 square kilometer in an Advanced Very High Resolution Radiometer [see Krzysik, Chpt. 42, this volume] remotely sensed satellite image or sampling 1-square-meter quadrats for herbaceous plants).

Accuracy and Precision. The cost of a project is directly related to the accuracy and precision (repeatability) desired. High accuracy requires high precision, while measurements that are highly precise and possess low variance (sampling error) may not be accurate. Accuracy requires that the experimentally derived statistic is close to the "actual value." Accuracy and precision are mainly dependent on the phenomena under investigation. But also important is the experimental or sampling design and sample size. In other words, a poor design may be overcome with high sample sizes, or even better, fewer samples are usually required by a superior sampling design.

An important component of any project is the reporting of sampling or measurement error. A number of terms can be used, and the appropriate one is usually dictated by the project objectives and other specifics. Common statistics include variance, standard deviation, standard error, confidence interval, and coefficient of variation. It is important to report sample size, and sample size is required to convert between values of standard deviation and standard error.

Conceptualization. Project conceptualization means explorations or discussions of ideas with peers or expert consultants and a thorough literature review. The literature review should not be limited only to the subject material directly related to the project, but other potentially relevant literature sources in other disciplines should be searched. Experience and peer consultation are important at this stage.

Design. The design phase is highly project specific and directly dependent on objectives, scale and resolution, and accuracy and precision. The design phase may include experimental design, ecological design, and sampling design.

Field Methods. Field methods, or the implementation of the design, are directly dependent on objectives, scale and resolution, and accuracy and precision desired. They may also depend on the design. A frequent mistake is the confusion of using common methods and collecting common parameters. For example, say that you want to monitor changes in vegetation structure (physiognomy) throughout the United States in all representative plant communities. Canopy cover is an important environmental parameter in this context in any ecosystem. However, it is erroneously believed that only one method should be used throughout the sampling universe to measure this parameter. In reality, the parameter canopy cover should be measured in all ecosystems, but the method used depends upon the magnitude of canopy cover (e.g., 5 or 95 percent), its spatial variance and patchiness, its height, and plant form. We need different methods in different ecosystems because we want to optimize sampling efficiency, accuracy, and precision within each of the unique spatial contexts presented in each ecosystem. The consistent and accurate estimation of parameters with known sampling error is the important factor, not consistent methods. Another important consideration, not often recognized, is that individual field personnel may prefer or be experienced with specific techniques, and therefore sampling efficiency is improved.

Professional Review. At this stage it may be desirable to obtain a peer or expert review from one or more specialists who have had previous experience in similar projects before additional expenses are incurred or an invalid approach is implemented. These reviewers should have expertise in field ecology (including geographical and local habitats), expertise in statistical design/analysis, relevant taxonomy expertise, and project-specific specialties.

Economic and QAC Analyses. The economic and Quality Assurance and Control (QAC) analyses component is critical to the overall success of the project yet is usually overlooked or disregarded as being unimportant. A thorough economic analysis of the complete cost of the project is essential. If the project is allowed to proceed without adequate budget commitments, one or more of the following will of necessity be compromised (often severely): objectives, scale/resolution, accuracy or precision, design, field methods. A QAC analysis is necessary for minimizing procedural error. Procedural error refers to poor, sloppy, or inconsistent field techniques, calibrations, recording of data, and field notes; excessive fatigue; or just plain mistakes regarding data quality. For example, I have heard of a field crew that used machetes to get through the dense brush in placing permanent transects for monitoring vegetation, while a second crew was responsible for estimating habitat parameters along the same transects. Procedural errors usually produce greater errors than sampling (measurement) errors, and 100 percent surveys are often less accurate than well-designed sampling schemes because more effort may increase procedural error. Furthermore, procedural errors cannot be assessed with statistics, which deal only with sampling errors.

Reality Adjustments. Continuing a project while violating economic reality almost always means project failure or at best an exceedingly poor cost-benefit return. At this stage only three alternatives are possible: change objectives and/or scale/resolution and/or accuracy/precision, which usually requires changing the design and/or field methods; get more money; or quit.

It is inappropriate and invalid to make a project more economical by changing the design or field methods while maintaining original objectives, scale/resolution, and accuracy/precision, because by definition the original design and field methods were optimized to provide ecological validity, statistical sufficiency, and sampling economy, while meeting specified project objectives.

Professional Review. A peer or expert review is critical at this stage because the project is ready for implementation with economic and QAC analysis available.

Pilot Study. If the project is of such magnitude and scope that it represents a significant or exceptional commitment of resources in terms of dollars and personnel, then a pilot study is highly recommended to evaluate the design, field methods, logistics, and economics. A pilot study is important for at least six reasons: it is usually needed to obtain design parameters and identify details in field methods; it assesses project feasibility; it assesses economics and QAC; it identifies problem areas, unforeseen circumstances, or the unpredictable logistics of field projects; it provides data to assess or model project feasibility, realities of objectives, design parameters, and field methods; and it provides the foundations for database management.

Professional Review. A peer or expert review is desirable at this stage to assess the success and problem components of the pilot study, including an independent assessment of the success of the design and field methods to meet desired objectives and design parameters.

Implementation: Stage I. Stage I implementation represents a full-scale demonstration project and is used as a final test of project feasibility and economics. It also represents the final fine-tuning of the design and field methods, with lessons learned from the pilot study.

Professional Review. As in reviewing the pilot study results, it is important to receive an independent review of the demonstration project.

Implementation: Stage II. Stage II implementation represents the final and complete monitoring program. Care must be taken to adhere to final decided objectives and all lessons learned from the peer or expert reviewed pilot and demonstration projects. The continuation of QAC in both fieldwork and database management is important.

Analysis, Modeling, or Hypothesis Testing. The analysis, modeling, or hypothesis-testing phases of the project follow directly from the conceptualization and design phases and are directly related to project objectives.

Interpretation. Interpretation logically follows analysis, modeling, or hypothesis testing relative to the stated objectives of the project. It is dependent on the training, experience, knowledge base, and familiarity with the literature by the principal investigators and consultants working on the project.

Literature Search. The results of the analysis, modeling, or hypothesis testing and subsequent interpretation develop new knowledge and new questions. In this new light, an additional literature search is required.

Synthesis. The interpretation and additional information gained from the literature leads to the next logical step—the synthesis of all relevant information, both new and old, to fulfill or complete the objectives and goals of the project.

Preparation and Presentation of Results, Professional Meetings, Symposiums, Seminars, and Workshops. The synthesis is not the final step in the project but leads to the presentation of project findings and results at professional society meetings, symposia, seminars, or workshops. This is also the time for the preparation of technical reports, professional manuscripts, or books. The exact nature is completely dependent on project specifics.

Peer Review. Peer review follows the preparation of manuscripts, book chapters, and presentations.

Publications and Presentations. The relative technical merits or scientific relevance of the project may vary enormously, depending on which of the phases discussed above were most worthy. It may be that the sampling design, the development of new field methods, a novel modeling technique, or new methods of database management were the most relevant.

Conclusions and General Recommendations

1. Use common sense and clearly explain the hows and whys of your experiment: ecological design, statistical analyses, assumptions and how they were evaluated (tested) and met or compromised, spatial and temporal arrangements and details, sample sizes, degrees of freedom, statistical power, and treatment replicates.

2. State objectives clearly and stick to them. Probably the most common violation in monitoring programs is the poor, vague, unfocused, unrealistic, too general, or catch-all formulation of objectives. Sometimes projects will proceed without sponsor, peer group, and investigator's consensus. Sometimes objectives will be changed after the project design and implementation. All of these factors jeopardize the applicability of the original project design and analysis criteria. Therefore, the validity of project findings are tenuous. Clear statements of objectives are important for your audience, including reviewers and editors.

3. In the design and analysis of projects of any scope and magnitude, think a priori. On the contrary, data analyses procedures in most studies are determined a posteriori.

4. Take advantage of your expertise. You know the most about your project and the specific spatial, temporal, and taxa issues involved. It has been my experience that an experienced field biologist with some fundamental knowledge of good sampling design designs better and more practical field studies than a professional statistician with no field experience in the specific study being addressed. Particular field knowledge that is important in study design includes spatial heterogeneity and patterns, organism distribution patterns, sampling intensity requirements, execution or procedural error potential, and field logistics and techniques required.

5. Learn the fundamentals of experimental and sampling design.

6. Systematic (bias) and procedural errors are important in the execution of field sampling. These errors not only extend beyond statistical analysis but are usually difficult to recognize, especially by readers, reviewers, and editors.

7. Do a pilot study. This is a critical step in any project and could save a great deal of time and money. The pilot study generates estimates of design and analysis parameters (e.g., required sample sizes, sample stratification and efficiency, appropriateness of statistical methods) and identifies implementation problems (e.g., quality assurance and control, field logistics, methods).

8. Own more than one statistics book and be familiar with contemporary design and analysis issues, such as where there is consensus and where there is controversy.

9. Learn where and how to find and use information. Libraries provide books, journals, reports, and computer search services. Government agency reports are valuable sources of information and actual data and may provide especially detailed descriptions of experimental and sampling designs, analysis methods and justifications, and field methods. The Internet and its World Wide Web are exponentially becoming a source of information and data but need a great deal of refinement to increase their efficiency at locating specific data requirements.

10. Become familiar with experiments, sampling designs, and statistical methods in other disciplines. Today is the realm of the specialist. However, if you broaden your horizons, you can apply developments in other fields to advance your own discipline. The model used for producing a landscape surface of the distribution and density patterns of desert tortoise (*Gopherus agassizii*) populations (see Krzysik, Chpt. 42, this volume) was originally developed for hydrological modeling of soil erosion and sediment yields. Field ecology is particularly closely related to many disciplines, including geography, geology, hydrology, soil sciences, paleontology,

meteorology/climatology, and many areas of chemistry and physics.

11. Do not believe everything you read. Use common sense and think critically. Just because a journal article is peer reviewed does not guarantee its conclusions, or even that there is universal consensus in the research or resource management community. Due to today's high degree of specialization, it is not uncommon for cliques of reviewers to review each other's manuscripts. Peer-reviewed literature is not all good, and gray literature is not all bad (see Resetar, Chpt. 40, this volume). Agency and consultant reports are considered gray literature because in the majority of cases they receive little or no formal review.

12. Do not overdo statistics. In trying to influence and convince your audience, simplicity and directness are best, especially with administrators, policy makers, and decision makers. It is easy to lose the crowd in even simple statistical demonstrations and the subtleness of Type I and Type II errors and statistical significance, much less the intricacies of complex factorial designs and multivariate statistics. When the differences between population means greatly exceed standard deviations, graphical displays and not statistical inference are in order. Graphical displays should always be used for communicating statistical results and summaries, while tables should rarely be used (tables belong in an appendix for casual or intimate personal perusal). Typically the mean and its standard deviation (or confidence interval) and sample size are the desired statistics. The sample size must always be included so the reader can calculate standard errors, confidence intervals, and degrees of freedom.

13. In statistical analysis, there has been too much emphasis on inference and not enough attention paid to exploratory or descriptive statistics. Significance tests and p-values have been overused. Although this paradigm represents mainstream statistical analysis and all practitioners are guilty as charged, statisticians have been warning of the pitfalls for over a half century. There has been a mind-set that has pervaded ecology (possibly physics envy) that inference and hypothesis testing are the real science in ecology, while exploratory, descriptive, or graphical statistics are not. Data testing and the clear communication of data, interpretations, trends, and relevant summaries to policy makers and decision makers are equally important.

14. There is an important difference between biological or ecological significance and statistical significance, although this is often overlooked. Biological or ecological significance represents biological realism and common sense directly relevant to actual ecological systems. Statistical significance is only relevant to sample size in the specific context of the probability of finding an observed difference by chance alone relative to the inherent variability in the system under investigation.

Summary

This chapter identifies some important principles and issues in experimental design and statistical analysis relevant to field biologists and ecologists, researchers, and environmental managers designing and implementing ecological assessment or monitoring programs. The emphasis is on areas of common pitfalls, confusion, and misapplications. A rich and diverse source of literature is provided. Topics covered include issues and approaches to statistical analyses, efficient statistical inference, statistical power, the abuse of statistical significance tests, issues in experimental design, pseudoreplication, sampling design, basic principles of ecological design and analysis, common problems in ecological design and analysis, and general recommendations. General principles are developed for designing and implementing an ecological or environmental monitoring program. The term "ecological design," when used in the context of ecological field experiments or ecological and environmental assessment and monitoring protocols, is recommended as a less ambiguous replacement for the following terminology: experimental design, quasi-experimental design, sampling design, or research design.

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Geographic Information Systems, Landscape Ecology, and Spatial Modeling

Anthony J. Krzysik

The objective of this chapter is to introduce the technologies and applications of Geographic Information Systems (GIS), landscape ecology, and spatial modeling to field biologists and herpetologists. The approach is to provide fundamental concepts, examples of applications, and a great deal of selected references for both concepts and examples. A detailed example is presented for spatial modeling of the distribution/density patterns of a vertebrate population on landscape scales by using an interpolation-smoothing algorithm originally developed for hydrological and sediment-yield modeling.

Field herpetologists best know their populations, communities, and specific nuances of habitat. The motivation for this chapter was that the information presented would enable them to reflect on their research design problems and needs and ask more interdisciplinary questions; dig deeper into the literature in unfamiliar books, reports, and journals; and acquire new technologies for their toolbox. In the spatial-temporal context provided by these technologies, important strategies, analyses, and methods could be developed, including identification of appropriate (or inappropriate) habitat features (parameters, elements, patterns), sampling design and site selection, predictive capabilities for taxa distribution, assessment and monitoring of populations, and visual interpretations and demonstrations.

Cartography, or mapping, has played an important role in understanding the ecology and classification of natural systems (Tosi 1964; Wikin and Ironside 1977; Brown et al. 1979, 1980; Bailey 1980, 1983, 1987, 1988, 1996; Rowe and Sheard 1981; Driscoll et al. 1984; Kuchler and Zonneveld 1988). A good introduction for field ecologists and biologists for land surveying and using a compass is Sipe (1979), and a review of methods for mapping and surveying is provided by Ritchie et al. (1988).

Excellent introductions to GIS, the technologies involved, and GIS applications are available (Burrough 1986; Star and Estes 1990; Tomlin 1990; Antenucci et al. 1991; Aronoff 1991; Maguire 1991; Bernhardsen 1992; Johnson et al. 1992; Laurini and Thompson 1992; Berry 1993; Environmental Systems Research Institute [ESRI] 1993; McLaren and Braun 1993; Haines-Young et al. 1993; Korte 1994). Another excellent, but expensive, advanced comprehensive review and encyclopedic treatment is Maguire et al. (1991a,b). There are even books available to assist project managers and administrators in GIS-related issues (Aronoff 1991; Cassettari 1993; Obermeyer and Pinto 1994; Polaris Conferences 1994; Huxhold and Levinson 1995). Maguire et al. (1991c) provide a summary of available textbooks and professional journals that are devoted to GIS.

The integration of GIS with knowledge-based systems (Coulson et al. 1987; Coulson et al. 1991; Smith and Jiang 1991) or with a suite of remote sensing, statistical analysis, ecological modeling, and traditional software (e.g., word processing, spreadsheet, database management) modules (Skole et al. 1993) has a great deal of potential for natural resources management. A comprehensive survey of GIS applications in environmental modeling is presented in Goodchild et al. (1993, 1996).

What Are GIS?

GIS are computer systems consisting of hardware and software for the purpose of inputting, storing, manipulating, classifying, transforming, analyzing, modeling, summarizing, and displaying spatially referenced data and information. Information systems can be defined as a collection of data and tools (e.g., hardware and software) for the purpose of deriving "information" that is not readily apparent from the individual data elements in the database (Laurini and Thompson 1992). Typical and powerful platforms for GIS are minicomputers, a popular one being the Sun-SPARC workstation. GIS are also available for PC and Macintosh microcomputers, including versions of minicomputer-based systems. Microcomputers have reached the speeds, memory, and hard drive capabilities of former minicomputer workstations, and the trend continues. Widespread and routine applications of GIS by nonspecialists may depend on these microcomputer platforms.

GIS are information systems that include quantitative spatial data (parameters for location, position, topological connections, and spatial relationships) and qualitative descriptive data for attributes (information about the spatial parameters). GIS deal with spatially explicit data in a digitized format and combine and/or transform existing variables into new variables. GIS can theoretically be applied to any spatial scale, from solar, global, continental, and national to molecular-level topology, and everything in between. However, the problem with these extreme examples of scale is the acquisition, storage, and registration of accurate and relevant spatial data. Traditional uses for GIS are geographical applications at landscape and regional scales, but the use of GIS at continental and global scales is rapidly increasing as data sets become available and the storage of data at terrabyte capacity becomes more economical. A functional feature of GIS is to convert data among different map scales, cartographic projections, and geographic coordinate systems.

Maps and Scales

All maps must include a scale legend. Bar scales provide the exact linear relationship between distances on the map to actual distances on the earth's surface. An areal scale represents area and is therefore represented by squares or circles. A map scale of "2.64 inches equals 1 mile" means that a 1-inch distance between two points on the map indicates that the two points are in reality separated by 0.38 of a mile on the earth's surface. The scale in this particular example is referred to as 1:24,000 or 1/24,000 = 2.64 inches per mile/(12 inches per foot times 5,280 feet per mile). A map that was 80 centimeters by 80 centimeters at this scale would cover a total area of 364 kilometers. Table 42-1 shows common map scales, their linear equivalents, and typical applications. Table 42-2 defines spatial scales relevant to geographical ecology; see also Delcourt and Delcourt (1988) and Delcourt and Delcourt (1992). Fundamental introductions to using maps include American Society of Civil Engineers (1983), Thompson (1987), Monmonier (1991), Muehrcke and Muehrcke (1992), and Wood (1992). Aerial mapping is reviewed by Falkner (1994).

Global Reference System

Latitude and longitude can be used to locate exact positions on the earth's surface. Latitude circles are called parallels, and longitude circles are called meridians. Parallels and meridians form a gridded network called a graticule. Approaching the poles, circles of parallels become smaller and converge to form a point, and meridians become more closely spaced and similarly converge to a point. In reference to the earth's axis passing through the poles, the origin of the latitude-longitude coordinate system (0, 0) is the intersection of the equator and the prime meridian. The most commonly used reference for the prime meridian is the Greenwich Prime Meridian, which passes through Greenwich, England. Latitude and longitude are traditionally measured in degrees, minutes, and seconds. For latitude, 0° is at the equator, 90° is at the North Pole, and -90° is at the South Pole. For longitude, the 0° meridian begins at the North Pole, passes through Greenwich, and ends at the South Pole. Longitude is measured positively up to 180° east of Greenwich and negatively up to 180° west of Greenwich. Some countries may use different prime meridians.

Longitude and latitude cannot be used to measure distances on the earth's surface. In this spherical coordinate system, positions are related to angles from the earth's center, while accurate distance metrics require a planar coordinate system. Only along the equator does the distance associated with one degree of longitude approximate the distance associated with one degree of latitude, because the equator is the only parallel whose radius equals that of meridians. This Global Reference System is not a map projection (discussed in a later section) but serves as reference positions on the earth's surface for all available map projections.

Table 42-1. Common map scales, map to landscape relationships, and typical map uses. Data from Ruiz and Messersmith (1990).

Map Scale	Cm/Km[1]	Inches/Mile	Typical Map Uses
1:1,200	83.35	52.80	Master planning
1:4,800	20.84	13.20	Master planning
1:15,840	6.314	4.000	Foresters and SCS[2]
1:20,000	5.001	3.168	SCS soil maps
1:24,000	4.168	2.640	USGS[3] 7.5' maps
1:25,000	4.000	2.534	DMA[4] special maps
1:50,000	2.000	1.267	DMA special maps
1:62,500	1.601	1.014	USGS, 15' maps
1:100,000	0.999	0.633	USGS, 30' x 1°
1:250,000	0.399	0.253	USGS, 1° x 2°
1:1,000,000	0.0995	0.063	USGS, 4° x 6°
1:2,000,000	0.0505	0.032	USGS, National Atlas

[1] Data calculated from inches/mile column.
[2] SCS = Soil Conservation Service.
[3] USGS = U.S. Geological Survey.
[4] DMA = Defense Mapping Agency, Hydrographic/Topographic Center.

Cartographic Projections

Cartographic projection is a transformation process that produces a systematic arrangement of the earth's spherical or geographic coordinate system onto a plane (Dent 1990). In essence, a projection is the mathematical transformation or modeling of a three-dimensional surface (the earth) and representing it in two dimensions (a map). For spatial scales on the order of a few square kilometers, projection is unimportant, because the curvature of the earth is negligible for small areas. For spatial scales ranging from 1,000 to 100,000 square kilometers, map projection becomes necessary.

The interest in map projections coincided with the transition between the Middle Ages and the Renaissance (mid-1400s to mid-1600). Lambert developed at least seven map projections in 1772. The history of cartographic projection is extensively summarized in Snyder (1993).

The earth is usually depicted as a smooth sphere, where planar intersections produce circles. In reality, the surface of the earth is highly irregular because of variations in gravity, crust thickness, rock or mineral density, and topography. Additionally, rotational centrifugal forces make the earth bulge at the equator and flatten at the poles. For small-scale maps, the representation of the earth as a sphere is adequate, but for large-scale maps (i.e., 1:1,000,000 or more) the earth must be represented as a spheroid (ellipsoid) with major and minor axes of different diameters (semimajor and semiminor refer to radii) and where planar intersections produce ellipses. The most commonly used parameters for spheroid representation of the earth were surveyed by Clarke in 1866 and are known as the North American Datum 1927 (NAD27). Recently, satellite-measured spheroids are starting to replace ground-based measurements. The ARC/INFO GIS support twenty-six reference spheroids.

Cartographic projection distorts one or more of the properties of shape, area, distance, or direction. Maps can be made using specific projections that preserve desired properties. Conformal maps preserve shape at local scales (no map projection can preserve shapes at large scales), equal-area maps maintain areas at the same map scale, equidistant maps preserve distances between specified points, and true-direction or azimuthal projections give the correct directions or azimuths of all points on the map with respect to its center. The map legend should provide the name of the projection used, along with relevant parameters. The ARC/INFO GIS support over forty-six projections.

Map projections are classified by the projection surface used. Conic, cylindrical, and planar are surfaces

Table 42-2. Definition of scale and associated terminology

Scale	Terminology	Spatial Extent (km^2)	Map Scale	Environmental Features
Micro	Habitat	< 1	< 1:1000	Microhabitats
Meso	Landscape	1–10^4	1:1000–1:100,000	Pattern-mosaics, environmental gradients
Macro	Regional	10^4–10^6	1:100,000–1:1,000,000	Physiography, elevation
Mega	Global	> 10^6	> 1:1,000,000	Ecoregions

Notes: Scale terminology from Delcourt and Delcourt (1988). Local scales refer to the smaller range of landscape scales. Map scale based on the entire spatial extent occupying a 1-by-1-meter map.

most commonly used because they can be flattened without surface distortion, but other classes of projections for specific applications are also possible. Another consideration is the nature of the contact of the projection surface with the sphere (earth). For example, imagine placing a tennis ball (representing the earth) on a large ice-cream cone whose opening is the same size as the tennis ball. This represents a conic projection tangent at the equator (or any latitude could be used, comparable to using a smaller cone), and the tangential circular line is called the standard parallel. Parallel lines of latitude are projected onto the cone as rings, while meridians (longitude) are projected that converge at the apex. The cone can be cut at any desired meridian to produce the final conic projection. The meridian opposite the cut becomes the central meridian. Because distortion increases north and south of the tangency parallel, this projection would be more useful for midlatitude zones. A more complex conic projection, a secant conic projection, could intersect the globe at two locations and would be defined by two standard parallels. Imagine the ice-cream cone centered on a holographic image of a tennis ball. A still more complex conic projection, an oblique conic projection, would be produced when the cone axis does not line up with the global polar axis. An equidistant conic projection would have evenly spaced parallels and would represent equal distances in the north-south directions, but the projection would not be conformal or equal-area. In the Lambert Conic Conformal projection, the central parallels are spaced closer than those at the border, preserving small geographic shapes. The Albers Equal-Area Conic projection spaces northern and southern parallels closer than the central parallels and displays equivalent areas.

Cylindrical projections (a cylinder replaces the cone) can also have a tangency line or two secancy lines around the globe. Two commonly used cylindrical projections are the Mercator and Transverse Mercator. In Mercator projections, the equator represents the line of tangency (cylinder parallel to polar axis), and the meridians are equally spaced (true east and west scales). In Transverse Mercator projections, meridians are used as the lines of tangency (cylinder perpendicular to polar axis), and parallels remain equally spaced (true north and south scales). Secant intersections and oblique cylinder projections are also possible, as in conic projections.

Planar projections (azimuthal) represent a plane touching the globe (tangent point) with polar, equatorial, or oblique aspects. The polar planar projection is commonly used in polar regions. Secant projections are not commonly used and represent the intersection of the plane and globe. The perspective from which spherical data are projected onto a flat surface determines spatial distortion. There are three perspectives used in planar projections: gnomonic projection—center of the earth; stereographic projection—the surface point directly opposite the tangential point (i.e., the South Pole if the planar contact was the North Pole); or orthographic projection—"infinity," a point external from the globe such as a planet or satellite.

For larger scales, such as those on the order of 1:500,000 or 1:1,000,000 or more, projections such as the Albers Equal-Area Conic or Lambert Azimuthal Equal-Area are used to minimize distortion in topological features (Star and Estes 1990).

For additional details and information concerning cartographic projections see American Cartographic

Association (1986, 1988), Snyder (1987, 1993), Dent (1990), Muehrcke and Muehrcke (1992), and ESRI (1994).

Geographic Coordinate Systems

Spatial analysis of GIS data requires that all map layers or themes must be registered to a common coordinate system. Registration represents the association of all parameters with a defined coordinate system or to a reference point, object, or grid that is registered to a coordinate system. The essence of GIS is that all input data are referenced to a two- or three-dimensional coordinate grid, and in all subsequent analyses or modeling, all data parameter sets are registered to identical reference coordinates, spatial scales, and cartographic projections to guarantee that output data are spatially accurate. There are four commonly used geographic coordinate systems.

Cartesian coordinate geometry is a system of intersecting perpendicular lines in plane space and the precise specification of location (Dent 1990). The Cartesian system is applicable in two or three dimensions with location points or raster cell (two-dimensional) data specified by x-y-z coordinates. Cartesian coordinates are useful for finding the relative distance and direction between two or more map features, but features cannot be directly related to specific features on the earth's surface unless the Cartesian system is itself geo-referenced. A common usage of Cartesian coordinates is with raw satellite imagery raster data (e.g., 20-meter, 80-meter, 1-kilometer cells), which eventually must be registered to specific earth features.

The Geographic or Latitude-Longitude coordinate system consists of parallels (latitude) and meridians (longitude), and coordinates are measured in degrees, minutes, and seconds. Any projection can be used for this grid, but in the Geographic Resources Analysis Support System (GRASS; see below), the Plate-Carree projection—where the equator is the standard parallel, the meridians are spaced the same distance as the parallels, and the origin is the intersection of the equator and the prime meridian (generally Greenwich, but prime meridians vary with countries)—is used. The projected grid consists of square cells, north-south coordinates range from 0° to 90°, and east-west coordinates range from 0° to 180°. For analysis and modeling applications, it is convenient to express values in decimal degrees, decimal minutes, or decimal seconds: 54° 20' 15" is equivalent to 54.334 degrees, 3260.25 minutes, or 195,615 seconds.

The State Plane coordinate system (SPCS) is a rectangular system of x-y coordinates defined by the U.S. Geological Survey (USGS) and is unique to each state. In order to minimize projection distortion, each state was divided into two to eight zones (Muehrcke and Muehrcke 1992). Each zone has its own central meridian, and the meridian's (false) origin is established in the southwest of the zone, usually 2 million feet (610 kilometers) west of the central meridian. States whose longest axis runs east-west (e.g., Iowa) use the Lambert Conformal Conic projection for a basis, while states whose longest axis runs north-south (e.g., Illinois) use the Transverse Mercator projection. Coordinates are measured in feet. On newer USGS 7.5' topo maps, SPCS tick marks are shown at 10,000-foot intervals.

The Universal Transverse Mercator (UTM) coordinate system is used for military maps, for spatial modeling, and commonly for maps representing scales of 1:1,000 to 1:250,000. The UTM system divides the earth into sixty longitudinal zones, each being 6° (360 divided by 60) of longitude in width and extending from 84° north to 80° south. The zones are numbered one to sixty eastward from the 180° meridian (e.g., 0° being the Greenwich meridian). Ten zones (numbers ten through nineteen) are represented in the United States, zone ten beginning at 126° longitude and zone nineteen ending at 66° longitude (Muehrcke and Muehrcke 1992). To minimize distortion, each zone is developed from a section of the ellipsoidal Transverse Mercator projection, known as the UTM projection. UTM coordinates are in meters and are referred to as easting and northing. The central meridian of each zone has an easting value of 500,000. Easting values greater than 500,000 lie east of the central meridian, while values less than 500,000 lie west of the central meridian. In the northern hemisphere, northing is expressed as the distance from the equator in meters. A UTM coordinate is identified by four values: easting, northing, zone, and hemisphere (e.g., 563,022E 3,777,019N 11N). The example used locates within 1 meter a Weber grill in the backyard of 61737 Apt. B, Desert Air Road, Joshua Tree, California, in the southern Mojave Desert. The coordinates were determined by a GPS (Global Positioning System), Rockwell International PLGR (Precision Lightweight GPS Receiver, AN/PSN-11). The accuracy is stated at ± 15 meters, but in calibration tests, consistent precision of 1 to 5 meters was achieved. UTM tick marks or grid lines are found on newer USGS 7.5' topo maps at 1,000-meter intervals.

Four other coordinate systems may have important specific applications: Local or Alphanumeric Grid, Universal Polar Stereographic (UPS), U.S. Army Military Grid Reference System (based on UTM and UPS), and World Geographical Reference System (GEOREF; Muehrcke and Muehrcke 1992).

Thematic Maps

GIS link map layers or themes of data/information. Each map layer is called a data layer, coverage, or thematic map. Thematic maps may represent vegetation or soil classifications, elevation, topographical features (slope, aspect), geological features, hydrology, species distributions, roads or utility lines, land use or ownership, political boundaries, or climatic parameters (Fig. 42-1). Thematic maps can represent choropleth or isopleth maps. Choropleths consist of polygons representing equal-valued parameters defined by sharp boundaries (e.g., counties or states) or at least the appearance of boundaries at the scale of coverage (e.g., plant communities or land-cover classes). Isopleths (isolines) display parameters by lines connecting points of equal value. Common geographical isopleths include topographic contours (elevation), temperature (annual mean, maximum, minimum), average degree days, number of annual frost-free days, mean annual precipitation, and annual potential or actual evapotranspiration. Thematic maps, therefore, consist of topologically linked geographic features and their descriptive data (attributes).

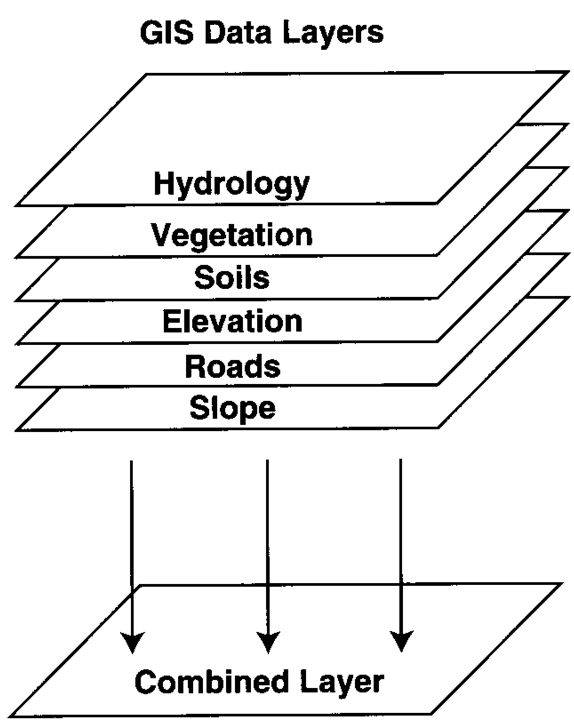

Figure 42-1. An illustration of GIS data layers, coverages, or thematic maps.

Vector and Raster GIS

GIS data can be inputted, stored, manipulated, and outputted in two fundamentally different ways, which are specific to the type of GIS used—raster or vector (McMaster and Shea 1992). In a raster-based system, each data point is represented by a cell located on a coordinate grid, and each cell has an attribute value. These grid cells are also known as pixels. Pixels, or picture elements, represent the smallest unit of information in a grid cell map or scanned image (Burrough 1986). In a vector-based system, data are stored in an x-y (and z for three-dimensional themes) coordinate system represented by the topological entities of points, arcs (lines), and polygons (areas). Each of these entities can possess attribute values. Modern GIS platforms have the capability to readily transform data between raster and vector modes using accessory modules, transforming codes, or proprietary software. Analyses and modeling in GIS projects routinely make use of both modes, because each has its respective strengths and weaknesses. Outputs and displays can be independent of mode of storage or manipulation of data.

Vector Data

Vector data themes are easy to illustrate because they directly relate to map features (Fig. 42-2). A map represents a set of points, lines, and areas that are defined by their spatial location with reference to a coordinate system and by their nonspatial or descriptor attributes (Burrough 1986). The map legend links these nonspatial attributes to spatial data. A region is a set of areas or map loci that are referenced to a single legend in a classification scheme.

Points are represented by single x-y coordinates and can represent springs, wells, mines, waterfalls, sampling stations, and museum specimen records.

Arcs, or lines, are defined as strings of x-y coordinates (vertices) that begin at one location and end at another, and connecting vertices create a line (ESRI 1993). Vertices define shape, and *nodes* define ends. Arcs are spatially defined by connectivity "to a node" (start) and "from a node" (finish) and by contiguity, possessing direction and left-right sides. Nodes are usually grouped into a list describing common attributes. Common ex-

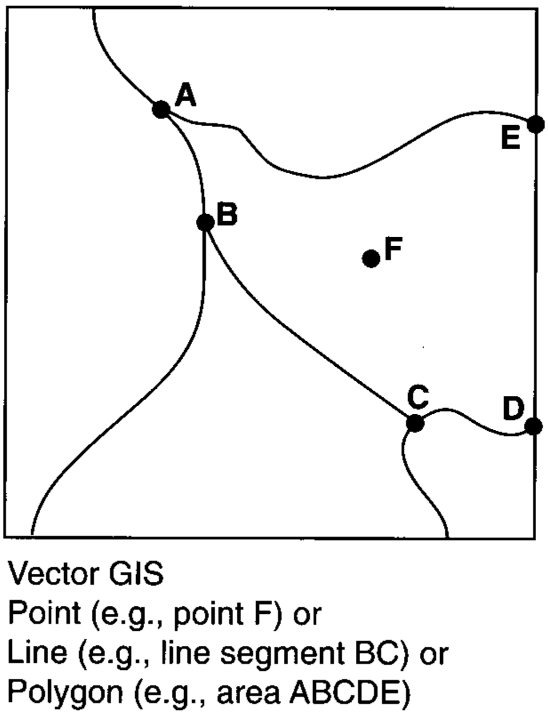

Figure 42-2. An illustration of vector-mode GIS.

amples of arcs include streams, roads, pipelines, power lines, and topographic contours of elevation.

Polygons are features defining a spatial area with coordinates forming an enclosed boundary. Polygons represent x-y line segments connected at nodes. Examples include states and counties, land use and ownership, bodies of water, toxic contaminated sites, and geographic ranges of species.

Topology is the spatial relationship between connecting or adjacent map features. It represents the essence of GIS function and commonly includes changing scales, combining adjacent polygons by decision rules, overlaying geographical and topological features, and modeling of paths through the landscape.

The modeling of paths through the landscape represents an important application of GIS, and some examples of path modeling will be discussed. The shortest route of least resistance, or more typically the path of fastest time or least cost (cost being defined by an explicit function related to landscape features), or even possible route between two points on a landscape is rarely a straight line. Considerations include pattern of roads and trails, topography (e.g., mountains, canyons), water, land use, and land ownership. Travel routes for deer or mountain lions may be dependent on riparian corridors or wooded steep ridges lacking housing developments. Dispersal of smoke plumes or aerosols will be dependent upon winds, thermal updrafts, and topography. Migration routes of anadromous fish will depend on dams, water quality, and instream flows. The successful migration of waterfowl and shore and wading birds through desert regions depends on the availability of wetlands and springs for feeding and resting.

Although arcs, nodes, polygons, and points are the main features of a coverage, six other features are used to completely define a coverage (ESRI 1993). Tics, or control points, represent geographic registration for a coordinate system. Annotations are the feature labels, such as the names of streams and roads. Links are rubber sheeting and adjustment for edge-mapping map sheets and other data adjustments. Routes are linear features composed of one or more arcs or portions of arcs. A section is an arc or portion of an arc to define a route.

Coverage extent defines the map boundary.

Raster Data

Raster data themes or layers represent information in a grid or cell structure (Fig. 42-3). The coordinate grid consists of square cells for spatial uniformity and simplicity in data handling. Actual raster cell sizes are user, project, or objective specific, but data availability, data storage capabilities, economics, time schedules, and practical considerations generally dictate raster resolu-

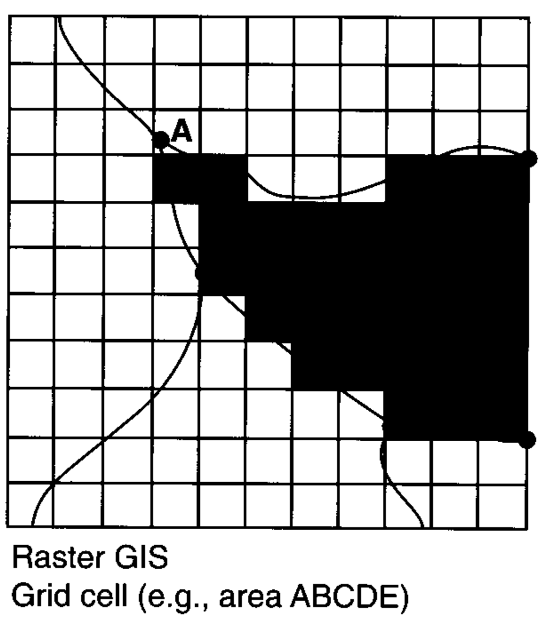

Figure 42-3. An illustration of raster-mode GIS.

tion. Remotely sensed satellite data, commonly used as themes in GIS analyses or modeling, use raster cell sizes that directly reflect the resolution (pixel sizes) of satellite multispectral data (Table 42-3).

Themes for raster cell data include qualitative/quantitative attribute classifications and satellite multispectral data. Raster cell data include soils, geology, vegetation classes (plant communities—series or associations), land cover (e.g., urban, agricultural, natural), and land ownership (e.g., federal, state, private). Each cell can possess a qualitative hierarchical attribute classification that includes an associated quantitative value for its specific classification. For example, in a raster thematic map representing Midwest vegetation, raster cells could be classified as:

1. forest or nonforest, at the coarsest hierarchy
2. forest, savanna, prairie, marshes, pasture, agriculture

At increasing hierarchies, forests could be further classified:

3. forest: deciduous, conifer, mixed
4. forest, deciduous: upland, bottomland
5. forest, deciduous, upland: oak-hickory, maple-beech, maple-basswood
6. further classifications based on subdominant tree species, understory characteristics, forest maturity, disturbance parameters

Additionally, within each of these qualitative classifications further quantitative classifications must be made for the raster cells:

1. bivariate—presence or absence (absence being defined by absolute absence or less than some threshold value)
2. ordinal—ranked value scales for presence or abundance
3. metric—actual or estimated metric values for density, cover, volume, frequency, dominance, importance values; in absolute or relative/percent metrics
4. probabilistic—some measure of the probability of occurrence above some threshold value

Table 42-4 contrasts vector and raster modes of GIS, giving the advantages and disadvantages of each.

GRASS, ARC/INFO, and ERDAS

The two most popular and largest GIS platforms are the raster-based GRASS, developed by the U.S. Army Corps of Engineers, Construction Engineering Research Laboratories (USACERL), Champaign, Illinois; and the vector-based ARC/INFO, commercially developed and marketed by ESRI, Redlands, California.

GRASS (USACERL 1993) conducts analyses in raster format, contains vector and point data programs, and possesses image-processing capabilities. ARC/INFO (ESRI 1993) conducts analyses in vector format and uses a GRID module based on GRASS code for raster capabilities. The analyses of enormous quantities of spatial data in multiple coverages are usually easier, more powerful, more efficient, and faster in raster modes. However, the recent advances in computer processing speeds and data storage capacities have shortened the "advantage gap" of raster systems. ARC/INFO has its own database module (INFO), while GRASS does not. GRASS was originally linked with RIM, which is outdated. ARC/INFO is closely tied with modern powerful database management systems such as Oracle and Informix, which greatly extend its capability to store and retrieve attribute databases rapidly and efficiently. Programs have been written in GRASS to access Informix databases. ARC/INFO is often used in conjunction with ERDAS (Earth Resources Data Analysis System, ERDAS, Inc., Atlanta, Georgia) to take advantage of ERDAS's raster analysis and image processing. Because satellite multispectral data are pixel-based, ERDAS's image-processing capabilities represent a powerful toolbox for inputting, analyzing, modeling, and outputting satellite imagery. A software product from ERDAS, IMAGINE, is marketed as a complete production and applications environment for simultaneous display and analyses of raster and vector databases—including satellite images, aerial photographs, thematic layers, vectors, and annotation—with subsequent map output (ERDAS 1993).

GRASS has traditionally been much easier to learn, understand, and use than ARC/INFO. However, with continuing developments at ESRI, this gap is narrowing. Table 42-5 presents the typical user manuals required for the two GIS.

GUIs (Graphical User Interfaces) are available for both systems. GUIs are user-friendly software programs with pull-down menus and point-and-click capabilities (e.g., Microsoft Windows®) that access and interface complex software systems that possess an extensive command language (e.g., GIS). The GIS GUIs are called XGRASS, GRASSLAND, and ARCVIEW and provide display and output capabilities of GIS formats. Although analyses and modeling capabilities are highly restricted, requiring the direct use of the parent systems, developments are continually progressing to extend GUI power and capabilities.

Table 42-3. Characteristics of four commonly used remote sensing multispectral satellite platforms. Data from Davis and Simonett (1991), Barrett and Curtis (1992), and Rock et al. (1993).

Satellite Sensor	Number of Bands	Spatial Resolution	Repeat Cycle	Spectra (μm)
SPOT (French)	1 3	10 m (panchromatic) 20 m	2.5 days 2.5 days	0.51–0.73 0.50–0.89
Landsat-TM (Thematic Mapper) (USA)	6 1	30 m 120 m (thermal)	16 days 16 days	0.45–2.35 10.4–11.7
Landsat-MSS (Multispectral Scanner) (USA)	4	80 m	16 days	0.50–1.1
NOAA-AVHRR (Advanced Very High Resolution Radiometer) (USA)	6	1.1 km	12 hours	0.60–1.1 and thermal

There are a large number of other GIS systems that are much less powerful (for typical applications) in analysis capabilities than GRASS and ARC/INFO. However, these other systems may be more economical, easier to use, or even better suited for specific applications. For example, there are many GIS platforms available for both PC and Macintosh environments that are much more economical but have limited capabilities. Examples for microcomputers include MAPINFO, MAPTITUDE, and PCARC/INFO. Software programs exist to enable both GRASS and ARC/INFO to function in the PC and Macintosh environments, but computer processor speed, memory requirements, and data storage capabilities typically necessitate the use of minicomputer workstations in these systems.

Because the GRASS GIS were developed by a federal agency, all software and associated source codes are in the public domain (free), and documentation is published at cost. However, the cost of computer hardware, operators, maintenance, training, and technical support can be substantial. Because ARC/INFO is a commercial platform, the cost of software, upgrades, and associated documentation is high, and the source code is not available for modification in user-specific applications. Nevertheless, the main costs typically associated with GIS projects are the acquisition of the appropriate or required data. The availability of data that are free or of low cost dramatically increases the economics of GIS.

GIS Input Data

Typical data for GIS are geographical, and therefore most GIS data layers represent the same information as that found in maps. However, maps represent analog data while GIS require digital data (McMaster and Shea 1992; Arlinghaus 1994). Analog data represent gradations such as signal strength and in maps or figures are represented as line thickness, shading, colors, etc. Digital data are the representation of numbers in the binary system, where any number or letter of the alphabet can be expressed in combinations of ones and zeros and therefore directly usable in modern computer systems. The digital format of GIS integrates geographic, cartographic, visual, and multispectral data with mathematical and statistical functionality. For example, the topographical surface of landscape patches can be defined by mathematical expressions. The first derivative of this surface map produces a slope map showing changes in elevation. The second derivative of the surface map produces a roughness map indicating changes in slope, which is directly analogous to an equation for distance traveled as a function of spatial geometry. The first de-

Table 42-4. Advantages and disadvantages of Vector and Raster GIS

Vector Mode GIS

Advantages
- Compact data structure
- Good representation of many kinds of data
  - Point attributes
  - Hydrography
  - Roads
  - Boundaries
  - Networks—utility lines, railroads
- Topology completely described with network nodes and linkages
- Necessary for network analyses
- Accurate graphics and high-quality line drawings
- Flexibility and generality in data retrieval, updating, and manipulations of graphics and attributes (may also apply to raster data)

Disadvantages
- Complex data structures
- Overlays of multiple vector polygon maps or polygon and raster maps may pose difficulties
- Modeling is complex, topological units vary
- Spatial analysis and filtering within polygons are impossible
- Poor flexibility and limitations for custom applications—no access to source codes for proprietary software (e.g., ESRI, ARC/INFO)
- Output display and plotting can be expensive, particularly if high resolution, color, and cross-hatching are desired (may also apply to raster data)
- Expensive software, especially if all software modules, raster capabilities, and remote-sensed image processing are desired (may also apply to raster data)

Raster Mode GIS

Advantages
- Simple data structures and inputs
- More power, efficiency, and speed for huge spatial databases and multiple coverages
- Directly compatible with remote sensed imagery, whose data are in pixels
- Applicable to spatial analysis
- Applicable to spatial and topological modeling
  - Inexpensive and quick overlays of map layer combinations
  - Used in Cellular automata
  - Spatial units same size and shape
  - Access to source codes for customizing user-specific applications if software is in the public domain (e.g., GRASS)
- Economical (GRASS software is in the public domain)

Disadvantages
- High storage capabilities required for graphic data
- Reduction in storage capacity results in loss of resolution (information)
- Output maps in raster format are crude in appearance (but depends on resolution)
- Difficulties with network linkages
- Time-consuming projection transformations (but depends on specific projects)
  - Need for specialized algorithms or hardware
  - Software modules required for handling points and arcs

Table 42-5. User's guides and reference manuals recommended by the developer for using GRASS (USACERL) and ARC/INFO (ESRI) GIS software

Recommended User Manual for GRASS GIS (available from U.S. Army Construction Engineering Research Laboratories, Champaign, Illinois)
GRASS Version 4.1 Geographic Resources Analysis Support System User's Reference Manual
Recommended User Manuals for ARC/INFO GIS (available from Environmental Systems Research Institute, Inc., Redlands, California)
Getting Started
What's New at ARC/INFO Version 7?
ARC/INFO Data Management
Map Projections: Georeferencing Spatial Data
ArcScan and Image Integration
Editing Coverages and Tables with ARCEDIT
COGO
ARCEDIT Commands
Map Display, Query and Output
ARCPLOT Commands
ArcStorm and Map Libraries
Managing Tabular Data
Data Conversions and Regions
GRID Commands
Cell Based Modeling with GRID
INFO
Network Analysis
ARC Commands
ArcTools
AML and FormEdit
AML Commands
System Administrator's Guide
License Manager's Guide
Supported Graphics Devices
Graphics Device Interface

rivative gives velocity, while the second gives acceleration, both as functions of spatial positions in a reference coordinate system. Although topography is an important coverage in GIS, other data are also relevant. Map information requires a two- or three-dimensional coordinate system where the following data may be represented.

Boundaries—political, land ownership, land use, geology, soil classifications, vegetation cover or classifications, water and wetlands, habitat disturbance, successional stages, species distributions.

Digital Line Graphs (DLGs)—one-dimensional lines in the landscape representing streams, rivers, fluvial channels, roads, utility corridors, and railroads. Although these attributes are in reality two-dimensional, their use is at a higher scale, and for practical considerations they are represented as lines.

Digital Elevation Models (DEMs)—are the digital representation of topographic maps. DEMs represent the three-dimensional topological surface or geomorphology of the landscape (see Table 42-6 for typical applications of DEMs).

Point attributes—represent specific user requirements, and as in DLGs, map scale is large compared to their surface area. Examples include springs or seeps, caves, mines, historical sites, and grave sites.

Important data layers or thematic maps in GIS include:

Existing maps—may represent from few to many coverages: political boundaries, land use, land ownership,

Table 42-6. Examples of applications of Digital Elevation Models (DEMs)

Topographic Contour Maps
Theme maps: elevation, slope, aspect, convexity, concavity
Shaded relief maps
Line of sight maps—cross-country visibility
Block: diagrams, profiles, horizons
Drainage networks
Drainage basin delineation—watersheds
Volume estimation
Model or estimate: runoff, erosion, and sediment yield or deposition
Civil engineering (e.g., road design, location of dams, hydrology)
Landscape architecture and regional planning (e.g., planning and design of landscapes, including urban)
Military applications (e.g., infantry, armor, and pilot training; weapon guidance systems)
Data for landscape and processes modeling
Data for geomorphology research
Data for integration with other thematic maps to produce desired products (e.g., LANDSAT TM, MSS, or AVHRR imagery to produce vegetation or land cover maps)
Attribute modeling (by designating elevation as a user-chosen continuous attribute variable, the DEM surface can represent a variety of features: travel time, cost or effort indices, weather phenomena, visual aesthetics, air pollution or temperature inversions, groundwater, landscape processes, etc.)

natural resources classifications, and management practices

Specialized GIS data—DEMs, DLGs

Digital photography—especially aerial

Remote sensed multispectral digital data—usually from satellite sensors but also from sensors mounted on or in aircraft

Collected field data—spatially referenced, usually with a GPS

Existing maps or photographs must be in a digital format for use in GIS. There are two ways to accomplish this, hand digitizing and electronic scanning. In digitizing, a map is laid perfectly flat on a large digitizing table expressly designed for this purpose, and a digitizing puck is manually used to trace boundaries of areas, elevation, or other contours, lines, and points of interest on the map. In scanning, a map, photograph, painting, figure, graph, or even text is put through a scanner, which transforms all visual information into digital format for magnetic storage on computer systems. Scanning technologies were not practical before modern, "reasonably priced" gigabyte and even terrabyte ultra high capacity storage devices became available, because even relatively simple pictures translate into an enormous amount of digital data.

Data input into modern GIS platforms include available magnetic media (usually tapes)—DEMs, DLGs, boundaries in digital format, satellite imagery; text files; data from digitizers; data from scanners; and interactive data input from keyboard or terminal.

GIS, DC, and CAD

Digital cartography (DC) is the storage of maps and their associated data in a digital format. GIS and DC have a number of features in common: both systems allow input and output editing; in both systems, attributes can be spatially associated; and both systems allow scale and projection changes.

Many map analysis features are not unique to GIS, but when processing time, commitment of resources, or very large scales are considered, GIS represent the only practical and economical alternative. Therefore, modern cartographic analysis and modeling are conducted in a GIS environment (Tomlin 1990).

Traditionally, Computer Aided Design (CAD) systems have been computerized drawing tools used in architecture and have not been used for analyses and modeling of attribute relationships that are spatially registered and referenced. However, modern CAD programs are incorporating GIS capabilities and vice versa (e.g., ARC/CAD).

Cowen (1988) and Parker (1988) provide additional discussions of GIS characteristics and compare GIS with other software systems.

Cartographic analysis and modeling commonly conducted in the GIS environment include:

1. overlays of two or more map layers to merge features spatially
2. updating of data
3. vector-raster transformations
4. buffering—to determine spatial proximity
5. masking—excluding areas from analysis, modeling, or outputs
6. averaging—any desired parameters and attributes
7. extraction of features
8. reclassification of map categories or polygons
    a. calculating areas
    b. averaging areas
    c. ranking, weighing schemes
    d. value, position, size attributes
    e. continuity, fragmentation measures
    f. shape—integrity; convexity, edge, ratio of perimeter to area; intrusion (nature of edges)
    g. pattern—mosaics.

A large number and variety of metrics and indices have been used to quantify landscape pattern and mosaics (See the section on Landscape Ecology [below] for a summary).

Important characteristics of GIS environments include:

1. multiple attribute associations with entities
2. manipulation, transformation, classification, storage, and output of relationships among entities
3. modeling and analyses among ecological elements or parameters and attributes (for a review of quantitative ecology see Legendre and Legendre 1983, 1987; Pielou 1984; Ludwig and Reynolds 1988; Krebs 1989; and Jongman et al. 1995)
4. optimization of spatially explicit metrics and measures
    a. distance
    b. ecological distance metrics or similarity indices (see Ludwig and Reynolds 1988; Krebs 1989)
    c. multivariate metrics (see Pimentel 1979; Dillon and Goldstein 1984; Pielou 1984)
    d. weighed statistical
    e. connectivity
    f. relationships
    g. cartographic neighborhood characterization
    h. spatial algorithms

GIS Capabilities

Important functions of GIS include location, spatial context, spatial pattern, attribute associations, temporal trends, and modeling and simulation. The following examples assume that the required databases, as well as the spatial analytical capabilities and associated algorithms, are available in the GIS platform. The examples used were made up to be illustrative but reflect and are comparable to realistic natural resources management or conservation biology research scenarios.

Location simply refers to the GIS database finding and displaying a desired attribute. Examples include: locate all the mines and springs in Vermillion County, Indiana, and locate the longest river confined to the state of Illinois.

Spatial context refers to location with conditional attribute features. Examples include: locate all lakes and reservoirs greater than 10 hectares in area that are between 10 and 100 kilometers from cities with populations greater than 100,000; locate all second-order stream segments that are downstream from urban developments with populations between 5,000 and 100,000; and locate all forest lands on north aspect 10 to 50 percent slopes that form riparian corridors that are greater than 100 meters in width on both sides of second- and third-order streams and are continuous for at least 2 kilometers.

Spatial pattern refers to the analytical quantification of size, shape, edges, fragmentation, distance, or pattern. Examples include: calculate the mean perimeter/area ratio of all forest patches in each 250-kilometer cell for the Midwest ecoregion grid; calculate the mean and standard error for the distance between forest patches for each county in Wisconsin; and calculate the fractal dimension and contagion for each cell in a specified gridded landscape.

There is a great deal of empirical evidence that the fractal dimension of landscape pattern decreases with increased anthropogenic activities, which can be attributed to landscape patterns becoming simpler and edges becoming straighter. Contagion is a measure of pattern in the landscape based on the probability of finding similar adjacent habitat patches from the pool of all possible habitat types in the landscape. In other words, do similar habitat patches have a tendency to clump, disperse, or occur at random? See the section on Landscape Ecology (below) for a list of potential metrics to quantify landscape pattern-mosaics. The list of potential quantifiable spatial parameters and patterns is limited only by the imagination of the investigator and the time or money to develop the necessary algorithms to carry out the calculations.

Attribute associations refer to combining location, spatial context, and/or spatial pattern to achieve a desired attribute. Recall that attributes are a parameter database associated with a spatial context. For example, from creel census data, what is the harvest rate (catch/person-hour) of smallmouth bass on second-order streams within 40 kilometers of cities with populations of less than 50,000 with respect to parameter RX (a designed analytical index to quantify the ecological condition of riparian habitats)?

Temporal trends refer to the monitoring of desired attributes. For example, what is the rate of deforestation (forest loss/year) in the tropics of Brazil per decade? The routine use of GIS for environmental time-series applications will continue to expand. Potential applications include: decreases/increases in habitats and ecosystems, habitat fragmentation and connectivity, changes in land use, monitoring restoration projects, dynamics of wildlife or biodiversity corridors, and monitoring ecosystem processes or degradation. John Anderson, U.S. Army Corps of Engineers, Topographic Engineering Center, Fort Belvoire, Virginia, is using aerial spectral photography (three bands) to successfully monitor the ecological condition of wetlands contaminated by organic pollutants or heavy metals (J. Anderson, personal communication).

Modeling and Simulation fundamentally refer to conducting "what if" scenarios in the context of geospatial relations, as discussed above, with specific attribute and/or spatially explicit models. For an extensive survey of environmental modeling applications, refer to the conference proceedings of "International Conference/Workshop on Integrating Geographic Information Systems and Environmental Modeling." The first conference, held in Boulder, Colorado, in 1991, established the foundation for Goodchild et al. (1993). The second conference was held at Breckenridge, Colorado, in 1993 (Goodchild et al. 1996). The third conference was held in Sante Fe, New Mexico, in 1996 (conference proceedings to be published).

Applications and Limitations of GIS

GIS are useful for any spatial data that require transforming, analysis, modeling, combining map layers, summarizing, or displaying. Therefore, GIS have potential applications in any technical field for diverse purposes. The theoretical potentials of GIS are virtually unlimited. However, the technical, practical, logistical, or economic constraints may often be formidable. Important uses of GIS and progress in their development have occurred in the following disciplines: the military; natural, earth, economic, social, and political sciences; and engineering. Activities for which GIS analysis and modeling are used include: management, planning, policy setting, decision making, research, and military activities. Typical applications of GIS have been with federal and state agencies and large consulting firms, where they have been used as important tools in managing natural resources (especially forestry), geological and soil resources, national parks and designated wilderness areas, urban and infrastructure development, and military training and testing lands. The potentials for the use of GIS in comprehensive regional planning are just being appreciated. The use of GIS in research has been limited. Possible reasons include high costs (hardware, software, personnel, data) and resource investments, highly specialized and dedicated operator skills, large data requirements, large-scale generalized databases, and unfamiliarity of traditional research disciplines with GIS technologies and platforms.

Although the use of GIS in the natural sciences has dramatically increased in the last few years, most technical papers in the natural sciences that deal with GIS are still found in specialized GIS or highly applied management journals. An examination of herpetology, ichthyology, avian, mammal, wildlife management, conservation biology, and ecology journals over the last five years discloses that only a few studies have used GIS technologies.

It is easy to become overly optimistic about the capabilities of GIS. However, GIS present serious concerns in many potential applications. The enthusiasm generated by vibrant and colorful large-scale maps and the desire for "quick fix" assessments or solutions to environmental and social issues on regional and global scales have facilitated the zealous "oversell" of GIS capabilities and economics (Aangeenbrug 1991). GIS applications and programs are associated with high investment costs: enormous database requirements for acquisition, input, and storage of data; hardware, software, and their maintenance; and the need for highly specialized, dedicated operators commanding a high salary in the current computer age. All of these factors have limited the routine use of GIS. The analysis and modeling of these enormous databases—including quality assurance in checking the validity and accuracy of input data, data transformations, use of accessory software, and obtaining the desired displays and hard copy outputs—are technically formidable, time-consuming, and expensive. Errors of accuracy, precision, and omission are common in spatial data sets (Crapper 1980; Goodchild and Gopal 1989; Chrisman 1991). The additive effects of errors at each thematic layer may drastically limit the accuracy, interpretation, or usefulness of the final product (Burrough 1989). The large number of colors or shadings necessary to represent the complex features and patterns in real-world landscapes has surpassed practical limitations for visual interpretation and additionally presents problems for copy reproductions.

GIS technologies are application tools that cannot replace field investigations, observations, and experiments, despite the claims of some enthusiastic proponents and administrators. Indeed, the success of GIS in any application is strongly and directly dependent on high-quality field data. Just as in statistical analysis, GIS cannot perform magic with poorly designed or carelessly executed inventories, assessment/monitoring programs, or field research. A commonly used metaphor in statistics is equally applicable to GIS: garbage in—garbage out.

Examples of GIS Applications

Remote Sensing

GIS and remote sensing technologies are commonly confused, and sometimes the two terms are used interchangeably. The two terms are not interchangeable. GIS are a separate and independent technology, often used without remotely sensed data. Although remote sensing preceded GIS, the primary current means of inputting, manipulating, analyzing, classifying, and outputting multispectral, remotely sensed data is integrating image-processing systems with raster mode GIS (Curran 1985; Ehlers et al. 1989; Ehlers et al. 1991; Davis et al. 1991; Davis and Simonett 1991; Faust et al. 1991). The value, utility, and interpretation of remotely sensed multispectral imagery are usually dependent on the use of ancillary GIS databases: DEMs, geology, soils, vegetation classifications, and ground field verifications. The classification of remotely sensed imagery into polygons or even into land cover without field verification is termed "unsupervised." Although this is often done, it is strongly discouraged. Satellite imagery may perform poorly for land cover classifications in situations where vegetation cover is sparse (e.g., arid landscapes), and even where vegetation is abundant the imagery may not be able to distinguish between vegetation types. In arid regions, geology profoundly affects spectral images, usually in complex, synergistic, and unpredictable ways. Even small amounts of some minerals or elements (e.g., iron) may affect imagery interpretation dramatically. Important considerations in classification include field verifications and analytical corrections applied to the imagery for atmospheric conditions, light reflectance and scatter, and topographic shadows. Field verification, especially in an iterative mode where repeated fieldwork keeps improving polygon classifications, is the recommended procedure and is termed "supervised" classification.

Remote sensing is usually associated with multispectral data obtained by satellite sensors (U.S. Army Topographic Engineering Center 1995). Table 42-3 summarizes the characteristics of four commonly used remote sensing satellite platforms. Remote sensing also includes aerial photography (color, black-and-white, and infrared), and specialized multispectral sensors can be mounted on aircraft or occasionally on air balloons. Scanners mounted on aircraft can achieve resolutions of 0.5 to 1 meter on the ground. The advantage of satellite sensors is their potential for addressing environmental issues at landscape, regional, continental, and global scales (Table 42-3). Excellent introductions and reviews of remote sensing technologies, capabilities, applications, and interpretations are provided by Campbell (1987), Mather (1987), Sabins (1987), Cracknell and Hayes (1991), Howard (1991), Quattrochi and Pelletier (1991), Barrett and Curtis (1992), Foody and Curran (1994), Lillesand and Kiefer (1994), USATEC (1995), and Verbyla (1995). Remote sensing has provided us with large-scale images of land use, vegetation coverages, land degradation, plant productivity, ecosystem properties, and landscape spatial and temporal patterns of patch mosaics and their boundaries.

Satellite sensors have been important in ecological assessment and monitoring: global ecosystem functions and processes (Hobbs and Mooney 1990), land cover on global scales (Tucker et al. 1986; Townshend and Justice 1988), tropical deforestation (Tucker et al. 1984; Woodwell et al. 1986; Nelson et al. 1987; Malingreau and Tucker 1988; Houghton et al. 1991), and forest declines in the northeastern United States (Vogelmann 1988, 1990; Vogelmann and Rock 1988; Rock et al. 1993) and Germany (Herrmann et al. 1988; Peterson et al. 1988). Remote sensing has also been extensively applied to the earth sciences, including global climatology, geology, hydrology, and oceanography (reviewed in Barrett and Curtis 1992).

An important application of remote sensing has been the capability for spatially and temporally monitoring primary productivity as a function of seasonality and land use using the NDVI (Normalized Difference Vegetation Index) calculated from AVHRR data (Jackson and Huete 1991).

$$NDVI = (B2 - B1)/(B2 + B1)$$

where B1 is the visible red band (580–680 nanometers) and B2 is the near infrared (725–1100 nanometers).

This index has been directly related to:

1. photosynthetic activity of vegetation and the leaf area index (Asrar et al. 1984; Tucker and Sellers 1986; Choudhury 1987)
2. vegetation biomass (Huete and Jackson 1987)
3. vegetation type (Tucker et al. 1985)
4. seasonality of global vegetation (Justice et al. 1985) and crops (Bartholome 1988)
5. grassland productivity and monitoring (Justice 1986)
6. vegetation patterns and biome comparisons between North and South America (Goward et al. 1985; Goward et al. 1987)
7. forest evapotranspiration patterns (Running and Nemani 1988; Nemani and Running 1989)
8. the ecology and epidemiology of the tsetse fly (Rogers and Randolph 1991; Rogers and Williams 1994)

Landscapes: Assessment, Monitoring, and Management

GIS have proved to be valuable tools in assessing and monitoring trends in landscape changes and their patterns from human activities (Iverson and Risser 1987; Iverson 1988), including regional effects of agriculture on water quality (Osborne and Wiley 1988; Johnston, Detenbeck, Bond, and Niemi 1990).

It is not appreciated that animals also represent major players in geomorphic (Butler 1995) and hydrologic (Johnston and Naiman 1987; Johnston 1994) changes in the landscape. Recent increases in beaver population growth has created new ponds at the rate of 0.0042 percent of the landscape per year, which is comparable to rates of anthropogenic changes in the landscape (Johnston 1994). The analysis and modeling of beaver-induced landscape changes by Johnston and her colleagues (Johnston and Naiman 1990a,b,c) represent a classic example of the utility of applying GIS technologies when studying large-scale landscape patterns, disturbance regimes, and ecosystem processes (Naiman et al. 1986; Naiman et al. 1988; Remillard et al. 1987).

It is becoming evident that natural resources need to be managed on larger scales, and the management of entire watersheds is such an approach (Naiman 1992; Satterlund and Adams 1992; Doppelt et al. 1993). GIS provide the capabilities for watershed delineations and monitoring a wide variety of ecosystem attributes and parameters as discussed above.

GIS have provided the foundations for analysis, visual display media, and map outputs for the U.S. Fish and Wildlife Service's National Wetlands Inventory Program.

GIS have probably been applied more to forest management than to any other natural resources discipline. An extensive review is presented by Sample (1994), who stresses the integration of GIS and remote sensing.

GIS technologies were the most important tools used for implementing the U.S. Environmental Protection Agency's Environmental Monitoring and Assessment Program (EMAP; Messer et al. 1991; White et al. 1992; O'Neill et al. 1994; see also Bowers et al., Chpt. 39, this volume). The stated goals of the program were to:

1. estimate the current status, trends, and changes in selected indicators of the condition of the nation's ecological resources on a regional basis with known confidence
2. estimate the geographic coverage and extent of the nation's ecological resources with known confidence
3. seek associations between selected indicators of natural and human stressors and indicators of the condition of ecological resources
4. provide annual statistical summaries and periodic assessments of the nation's ecological resources

Funding cuts have jeopardized the continuation of EMAP. A scientific review of the program is provided in National Research Council (1995).

Conservation Biology

The classic example of using GIS for conservation planning and setting management priorities is the U.S. Fish and Wildlife Service's GAP Analysis Program (GAP; Scott et al. 1993). To summarize briefly, the GAP GIS database is constructed from three primary coverages or thematic maps at the state level: (1) type of vegetation cover, (2) predicted animal distributions, and (3) land ownership. Data quality and resolution depend a great deal on the current status of state-specific databases, because no new field data are generated. Map layer one is primarily generated from Landsat TM imagery combined with DEMs and existing data on the state distribution of plant communities and their environmental preferences (e.g., elevation). Map layer two comes from the state natural heritage programs and consists of the distributional records of vertebrate species (Vertebrate Characterization Abstracts [VCA]), federal and state threatened/endangered (T/E [or listed]) species, and sometimes butterfly and T/E vascular plant species. Simple wildlife-vegetation models are usually applied to extrapolate to areas where distributional data are lacking. Map layer three represents a gradient in the level of habitat protection. National park and wilderness designations offer the highest levels of protection for resident habitats and biodiversity, while private lands offer the least. Multiple-use federal and state lands offer intermediate protection, which depends directly on site-specific management goals and objectives. These three coverages are used to construct a fourth layer, which geographically identifies "gaps" where listed species, rare species or ecosystems, species with small and limited geographical distributions, or specific species assemblages (communities) are not protected or only have limited protection. These data motivate land acquisition or nature reserve design based on corridor connectivity.

There is a fundamental problem with state natural heritage databases that is not generally appreciated or understood. This problem is independent of accuracy (taxa or location data) or quality assurance in database management. These databases are typically based on collections and not on samples. There is a profound difference between collections and samples based on statistical validity. Collection records are based on museum specimens, university collections or studies, and possibly data from state parks or nature preserves. These collections possess a strong bias for assessing actual spatial distributions (see also Resetar, Chpt. 40, this volume). For example, university field trips, research studies, or collecting trips are strongly dependent on convenience of distance traveled, location accessibility, familiarity with the region, and very importantly, success experienced in previous fieldwork. Museum collections have the same bias, particularly the latter, because a collector in a new region, in order to ensure success at obtaining desired specimens, may select collection sites based on the known success of previous collectors. It would be interesting to verify if biodiversity hot spots were located within 75 kilometers or so of universities. Additionally, because museum (and to some extent state) biologists desire county records, collection sites may be conveniently located near the intersections of several counties, irrespective and independent of the landscape spatial relationships between political and ecological boundaries. Samples, on the other hand, are based on a sampling design or experimental design for the specific purpose of avoiding bias and optimizing representation.

Satellite Telemetry

The integration of GIS and satellite telemetry receivers has enabled wildlife managers to assess and monitor home ranges and dispersal parameters of large vertebrates (Craighead et al. 1971; Amlaner and MacDonald 1980; Timko and Kolz 1982; Fancy et al. 1988; Fancy et al. 1989; Marsh and Rathbun 1990; Keating et al. 1991). GIS have also been used for database management, analyses, and presentation outputs of traditional radiotelemetry studies.

Economic

A traditional use for GIS has been in urban and regional planning (Maguire et al. 1991b). GIS have been used in a wide range of economic applications, from market analysis (Beaumont 1991) to predicting mineral deposits (Bonham-Carter et al. 1990; Bonham-Carter 1991).

Landscape Ecology

Landscape ecology is the study of ecological patterns in a geographic or spatial context and represents an interdisciplinary approach. Although in theory landscape ecology can be applied at any scale, traditional "landscape approaches" have been at meso scales, 1 to 10,000 square kilometers (Table 42-2). From my perspective, landscape ecology is synonymous with geographical ecology, but its interdisciplinary nature has polarized specific disciplines into each of these constructs. A great deal of the patterns that we see on the landscape are due to the activities of humans, resulting in habitat elimination, disturbance, degradation, and successional seres. Landscape ecology deals heavily with anthropogenic patterns, and therefore the disciplines of geography, landscape architecture, planning, engineering, and GIS computer technology are strongly represented. Geographical ecology is dominated by ecologists and other biologists (e.g., systematists) stressing the patterns or processes of ecological systems or taxonomic entities also in a geographic and spatial context.

Landscape ecology had its origins with German geographers in the 1950s and 1960s (Forman and Godron 1986) and is often closely integrated with GIS (Haines-Young et al. 1993). However, it has only recently received a great deal of attention and made appreciable advancements. This can be attributed to advances in GIS and the widespread availability of powerful minicomputer workstations. Another important motivation has been to comprehend and predict the accelerating degradation of natural systems and their patterns by anthropogenic stressors, particularly habitat loss and fragmentation. Landscape ecology is the discipline that deals with ecological phenomena at landscape or larger scales. These phenomena include all ecological attributes that are recognized at local scales: structure (including composition), function, processes, and interactions; these phenomena additionally encompass pattern and emphasize the context of space and time so relevant to large scales. Landscape ecology is more interdisciplinary than traditional ecology because of its natural association with geography, hydrology, geology, soils, climates, and especially GIS and their associated computer-intensive technologies, such as knowledge-based systems. As landscape ecology grades into regional scales, social and economic issues emerge, complicating science with policy and politically driven motivations.

The landscape ecology approach for natural resources research, monitoring, and management is essential for the successful persistence of populations, species, and communities and the ecosystem processes they depend on, including natural disturbance regimes. Excellent foundations and discussions of landscape ecology can be found in Forman and Godron (1986), Turner (1987, 1989), Zonneveld and Forman (1990), Kolasa and Pickett (1991), Turner and Gardner (1991a), Vos and Opdam (1993), and Forman (1995). Forman (1995) represents a current synthesis, containing 1,961 worldwide references. The ecology and physical geography of landscape boundaries and ecotones are important issues in current research (Holland et al. 1991; Furley et al. 1992; Hansen and di Castri 1992).

Landscapes consist primarily of three elements and the dynamics of their resulting patterns: patches, matrices, and corridors. The visual reality of boundaries or ecotones associated with these elements gives rise to the concept of mosaics. The interconnecting pattern of corridors are termed networks. Networks are characterized by linkages, nodes, intersections, and hierarchies (Forman 1995). Hierarchies are an important landscape feature and represent, for example, the dendritic pattern of stream orders. Landscape ecology is the study of the spatial and temporal structure and dynamics of pattern-mosaics and their boundaries, scale dependencies, and how these relate to the flow or movement (or cycling) of organisms, matter, energy, disturbance regimes, and anthropogenic stressors. A great deal of landscape ecology is devoted to quantifying and classifying all possible aspects of patches, matrices, corridors, and their resulting patterns and mosaics and will be discussed in the next section. GIS database development, modeling, and analysis have been instrumental in this research. The concepts of habitat patches, fragmentation, and their dynamics have a good ecological foundation (Burgess and Sharpe 1981; Harris 1984; Pickett and White 1985; Noss 1987; Shafer 1990; Shorrocks and Swingland 1990) and have their origins in island biogeography theory (MacArthur and Wilson 1967; Simberloff and Abele 1976).

Parks are patches of vegetation in a matrix of housing and infrastructure in an urban landscape. In the rural countryside of the Midwest, forest woodlots are patches in a matrix of row crops or pasture. The remaining old-growth forests of the Pacific Northwest are patches in a matrix of early succession forest, and in the southern Rocky Mountains of New Mexico roadless designated wilderness areas are patches in a matrix of multiple-use forestry covered with a dense network of roads.

Corridors are landscape elements that run through the matrix and connect patches. Important corridors are rivers and streams, with their riparian vegetation, or the ridges of mountain ranges. In human-dominated landscapes, fencerows, hedges, and shelterbelts are common features of the landscape. Corridors represent the most important movement, dispersal, and recolonization routes for vertebrates, invertebrates, plants, and undoubtedly microbes. Although corridors are typically ribbonlike in feature (Johnson 1989), corridors can represent the restoration of large areas to permit an ecologically functional link between large, fragmented ecosystem patches (Noss 1992; Noss and Cooperrider 1994).

Corridors are appreciated by professional wildlife managers and the public for their role in linking natural areas and providing habitat routes through urban areas or disturbed habitats, and the concept has been well discussed (Harris 1984; Adams and Dove 1989; Shafer 1990; Noss and Cooperrider 1994; Forman 1995). The benefits of corridors have been well articulated in reference to their use in core reserve design and in conjunction with buffers, multiple-use lands, and urbanization. Corridors are important for population dispersal, recolonization after local extinctions due to environmental catastrophes or deleterious demographic or genetic stochastic events, maintaining metapopulations, and providing valuable habitats (e.g., riparian ecosystems). In a general sense, corridors do not have to be linear but could effectively function where habitat patches form stepping stones for movements of organisms. For example, city parks in urban settings (e.g., Central Park in New York City) may represent valuable resting and feeding places for migratory birds.

Conceptually, landscape corridors have received strong support from land managers and conservation biologists. However, there have been a few skeptics. Simberloff (e.g., Simberloff et al. 1992) has criticized corridors on the following grounds: there is little empirical data or evidence to substantiate specific desired values; corridors could spread disease or disturbance regimes, for example, fire; corridors could disperse predators or act as ambush zones; corridors could provide habitat for weedy species and exotics; and corridors can be expensive to construct and maintain, and precious conservation dollars may be more cost-effectively used for other projects.

Grain is the finest level of spatial resolution in a given data set and represents pixel size for raster or multispectral satellite imagery. Extent is the largest spatial scale for consideration in the data set and usually represents the study area under investigation or duration of the time under consideration. Grain, extent, and other landscape ecology terminologies are discussed in an introductory framework by Turner and Gardner (1991b).

Quantifying Landscapes

Natural systems at all levels of ecological hierarchies (genes/populations, communities/ecosystems, ecoregions or biomes, and the biosphere) form complex and heterogeneous patterns on the landscape. These patterns are of two fundamental types, and both are strongly scale dependent—gradients and mosaics. Gradients represent gradual and more-or-less continuous spatial changes in landscape attributes; climate, soil moisture, general classes of soil types, general classes of vegetation, and species distributions are major examples. Mosaics represent abrupt changes in the landscape with discernable (visual or otherwise) boundaries. Important examples are vegetation, soils, some geological formations, aquatic-terrestrial edges, and riparian zones in arid regions. It should be obvious that any of the landscape attributes listed above can represent either gradients or mosaics or both, depending primarily on scale but also on site-specific conditions. Two important examples are microclimates, which can possess very sharp boundaries, and wetlands, which generally represent a complex of spatial and temporal mosaics and gradients of aquatic and terrestrial habitats instead of either a clear, discernable boundary or an obvious gradient, but either condition is also possible.

Environmental gradients have typically been analyzed and modeled by community ecologists, generally through ordination techniques (Whittaker 1982; Kershaw and Looney 1985; Digby and Kempton 1987; Feoli and Orlóci 1991; Kent and Coker 1992). The most fundamental analytical expression of an environmental gradient is a principal component solution (Krzysik 1987). The most useful techniques for environmental gradient analysis are: Principal Component Analysis (PCA; Pielou 1984; Digby and Kempton 1987), Correspondence Analysis (CA) or Reciprocal Averaging (RA; Hill 1973; Gauch et al. 1977; Greenacre 1984), Detrended Correspondence Analysis (DCA; Hill 1974; Hill and Gauch 1980; Gauch 1982), Canonical Correspondence Analysis (CCA; Ter Braak 1986, 1987; Jongman et al. 1995), and Nonmetric Multidimensional Scaling (NMDS; Kenkel and Orlóci 1986; Faith et al. 1987; Wartenberg et al. 1987; Young 1987). PCA and NMDS often produce comparable results. Pielou (1984) and Digby and Kempton (1987) provide lucid and fundamental introductions into PCA and CA for nonspecialists. All texts in multivariate statistics discuss PCA. Manly (1986) and James and McCulloch (1990) are excellent introductions to this field. PCA remains among the best ordination techniques and method to interpret environmental gradients, despite the new techniques and criticisms in the literature (e.g., Gauch 1982). Analytically, it is a direct and heuristically simple means for tracking and interpreting data variance patterns. DCA, on the other hand, relies on mathematical ad hoc "tweaking and adjustments" to produce "clearer" visual outputs, but possibly at a loss of realism and interpretation. Kenkel and Orlóci (1986) and Wartenberg et al. (1987) discuss shortcomings and interpretation problems with DCA.

The modeling and analysis of mosaics belong to the discipline of landscape ecology. A number of metrics have been suggested to quantify mosaic patterns. Forman (1995) provides a comprehensive review of analytical functions.

Patch Shape based on:

A. lengths of axes—(1) form, (2) elongation, (3) circularity

B. perimeter and area—(4) compactness, (5) circularity, (6) shoreline development (Patton's diversity)

C. area—(7) circularity, (8) circularity ratio

D. radii—(9) mean radius

E. area and length—(10) form ratio, (11) ellipticity index

F. perimeter—(12) shape factor

G. perimeter and length—(13) grain shape index

Mosaic metrics:

H. diversity measures—(14) relative richness, (15) relative evenness, (16) diversity, (17) dominance

I. boundary or edge measures—(18) edge number, (19) fractal dimension, (20) relative patchiness, (21) boundary length, (22) boundary density

J. patch-centered measures—(23) isolation of a patch, (24) accessibility of a patch

K. all-patch pattern measures—(25) dispersion of patches (aggregation), (26) isolation of patches (standard distance index), (27) nearest neighbor probabilities, (28) contagion, (29) patch density, (30) contiguity

Network metrics:

L. connectivity—(31) gamma index for network connectivity

M. circuitry—(32) alpha index for circuitry

Turner et al. (1991) reviewed analytical methods and statistical procedures for landscape-scale patterns and divided the technologies into two classes: those addressing patterns repeated in the landscape and those with patterns that vary in an irregular manner.

Landscape pattern quantifications have also been subjected to a large variety of texture measures (Musick and Grover 1991). Textures measures are particularly applicable to image processing of remote-sensed multispectral data.

Spatial Modeling

Spatial modeling represents a broad diversity of environmental and ecological applications (Turner 1992; Goodchild et al. 1993; Goodchild et al. 1996; Bonham-Carter 1994; Fotheringham and Rogerson 1994). This discussion will be limited to the interpolation and smoothing of geographic data for prediction, visual interpretations, and demonstrations. A common problem in spatial modeling is to construct a distribution and density surface for some parameter of interest where data are collected from spatially explicit sampling points. The parameters may be biological, geological, or geomorphic. Biological parameters include genetic structure, populations or metapopulations, species, or species assemblages (communities). Geological parameters include soils, substrate textures, and economic deposits of minerals and ores. Geomorphic surfaces are necessary for hydrological, erosional, and sediment transport modeling.

The simplest example of parameter fitting is the well-known two-dimensional least-squares fitting for producing a linear model (equation) from a scatter of data points (linear regression). Nonlinear trends can similarly be modeled with curves or splines derived from polynomial equations, although things become more complicated because one has to decide on the form of the model. Extensions to three (or more) dimensions, although directly comparable to the simple case, become much more complicated.

Surface modeling of geographical spatial data belongs in the realm of spatial statistics, or geostatistics, which has followed a course independent from traditional statistics, including the use of terminology. An important problem in spatial statistics is as follows. We have established a systematic sampling grid on a given region of the landscape and at each sampling point, transect, or quadrat we obtain a series of z values for the parameter of interest (e.g., density of frogs) over the entire region, each associated with grid coordinates x, y (i.e., easting and northing, respectively, in UTM coordinates). How do we interpolate to find the z values between our sampling stations and produce a smooth distribution/density surface that represents the closest unbiased fit to the actual data we collected? A common and practical example is the use of a DEM (Digital Elevation Model), where in this case x, y values represent isolines (contours) for constant values of z (elevation). After interpolation and smoothing, the resulting surface represents a realistic topology of the landscape and is useful to model precipitation runoff and sediment transport.

There are numerous benefits to such a spatial model.

The model visually summarizes data over a much larger scale than sampling alone would permit, economizes sampling effort, assesses spatial and temporal trends (when sampling is repeated), and makes predictions where there are no data. There are four major techniques for spatial interpolation and smoothing: trend surface analysis, moving averages analysis, kriging, and spline methods.

Trend surface analysis (Ripley 1981; Burrough 1986; Haining 1990; Turner et al. 1991; Jongman et al. 1995) is the extension of least-squares curve fitting to produce three-dimensional or any dimensional surfaces. This method is useful for showing broad, large-scale features of the data and emphasizes regional trends. Local trends are obscured. Trend surface analysis can also be used in preliminary analysis to remove "generalized features" from a data set, and then residuals can be analyzed using other multivariate methods. Residuals represent nonsystematic local variation. Trend surface analysis is restricted by the same assumptions as regression methods. Samples must be chosen at random, and the dependent variable (z) is assumed to be normally distributed with its variance independent of spatial context. These are restricted assumptions for geospatial data.

Moving averages analysis (Ripley 1981; Burrough 1986; Isaaks and Srivastava 1989; Haining 1990) is easy to visualize in the following example. Suppose we have sample values of parameter z that we collected along a transect at equidistant sampling points (x_i) and we want to estimate (predict) an unknown z value along the transect that lies between two sampled points. If parameter z represents a complex gradient along the transect, a simple average between the two adjacent known values would possess error. A better strategy would be to select a "window" that includes more than just the adjacent values and calculate the mean weighed by the distances to the known sampling points. The extension of this analogy to the two-dimensional plane is direct and intuitive, replacing x_i with the coordinate vector (x_i, y_i). Points characterized by many variables can be measured by Euclidean, Mahalanobis, Minkowski, Manhatten, etc. distance metrics (Pimentel 1979; Dillon and Goldstein 1984; Pielou 1984). Possibly, a wide range of similarity measures or distance coefficients may be applicable and innovative. Ludwig and Reynolds (1988) and Krebs (1989) provide a good discussion of these coefficients.

Estimates by moving averages are susceptible to clustered data points, but corrections can be made with distance-weighed least-squares methods (Ripley 1981). Of course, there are the problems associated with determining domain or window size, spacing, shape, and orientation, which influence analysis results, including whether local or large-scale variations or trends are emphasized. Because local maxima and minima of the interpolated smoothed surface are only associated with data points, various algorithms have been used to enhance the fit of data points to the surface using second derivatives or Hermitian polynomials (Burrough 1986).

Kriging (Ripley 1981; Burrough 1986; Isaaks and Srivastava 1989; Haining 1990; Webster and Oliver 1990; Cressie 1991) was named after a mining geologist who perfected a method to optimize gold ore extraction in South Africa (Krige 1966). Technically, the method is called the Wiener-Kolmogorov Prediction (Ripley 1981). It has been extensively applied in mining, geological explorations, and soil and groundwater mapping. Kriging is also known as optimal interpolation using spatial autocovariance, because it has its basis in regionalized variable theory. Kriging consists of a variety of methods and is the most widely known and applied geostatistical spatial interpolation technique. The theory assumes that spatial variation of a parameter is a mathematical function (model) of three components: a structural component with its associated constant mean value or a constant trend, a random spatially correlated component, and a random error component (noise). The result is a strong emphasis on spatial dependence between samples as measured by semivariance. Semivariance is a measure of the variance (variability) between sampling points as a function of distance between them and is estimated from the experimental data. The plot of semivariance versus sample spacing produces the semivariogram. The semivariogram is used to determine the weighing coefficients for local interpolation in a procedure similar to moving averages, except that the weights do not come from spatial distances but more appropriately from a statistical foundation (the geostatistical analysis) based on spatial variability (the sample semivariogram).

The advantages of kriging are significant. Kriging represents exact interpolation, because interpolation function values coincide with data point values. The use of spatial dependence in formulation dramatically improves local interpolation and therefore predictive capabilities. Probably of most significance is that kriging yields estimates of errors in interpolation and is the only method discussed that has this capability. The mapping of error terms gives valuable insight about the reliability of the interpolated values over the investigated region.

Kriging strongly depends on the fact that the calculated semivariogram is a true estimator of spatial covariation in an area. The presence of outliers in field data can overly influence the semivariogram and reduce the effectiveness of kriging. An important problem experienced by kriging is the violation of the intrinsic hypothesis (homogeneity of first differences). In other words, these are complex trends in the structure component and heterogeneity in spatial variability.

Spline methods (Ripley 1981; Burrough 1986; Wahba 1990; Cressie 1991) are also known as tessellations and triangulations. A draftsperson is intimately and empirically familiar with spline techniques using flexible rulers (splines) and eyeballing to produce smooth curves through scattered data points. In practice, small segments of curves are fit exactly with cubic spline functions, and in a similar fashion segments are fused to become continuous. The resulting curve with fitted equation parameters represents a continuous cubic polynomial that possesses continuous first and second derivatives. This detail is not possible with trend surface equations. Splines can be used for exact interpolation where the derived function passes through all data points, more typically for smoothing where it is desired to produce a trend curve (or surface), and for circumventing random error in the actual data points. The term "bicubic splines" is given to the three-dimensional case where surfaces instead of lines are interpolated and smoothed to fit data points. However, this surface cannot typically be defined by a single analytic function but can be represented as a mosaic of surface patches (plates) constructed from "spline curve segments." Spline methods are computer intensive, and their widespread use has been closely related to the availability of inexpensive high-speed minicomputers and, more recently, to current high-powered microcomputers.

The advantage of spline methods is that they retain local or small-scale features, in contrast to trend surface and moving averages analyses. Compared to moving averages, spline-fitted surfaces do not require additional adjustments in the vicinity of data points because the interpolated surface can lie on either side of the actual data points. They are also aesthetically pleasing and depict a good overview of data trends. Their main disadvantage is that there is no direct estimate of error terms in the interpolation. However, Dubrule (1984) has estimated error terms by jackknifing (a computer-intensive Monte Carlo resampling strategy for estimating statistical parameters from the original data; see Krzysik, Chpt. 41, this volume). There is also the problem of patch definition and how patches are "sewn" together without introducing extraneous anomalies. Another problem is deciding whether the interpolated surface should coincide with the data points or be interleaved. Each gives different results.

Kriging and spline methods are formally related, because all commonly used spline-based functions are generalized covariances (reviewed in Cressie 1991). These methods are also closely linked through Bayesian analysis (Kimeldorf and Wahba 1970).

Few published studies have compared the suitability of the various methods to the same data set. When splines and kriging were compared by Dubrule (1983, 1984), he concluded that splines produced more attractive maps, while kriging produced better quantitative results but was much more demanding of computer time. Burrough's (1986) table 8.3 provides a concise comparative summary of interpolation methods.

Example of a Landscape-Scale Spatial Model

Researchers at the U.S. Army–Construction Engineering Research Laboratories (USACERL) have been developing a novel technology to interpolate, smooth, and model geographical spatial data. The technique is Smoothing Thin-Plate Splines with Tension (TPS). Preliminary modeling results at USACERL and at Purdue University have shown advantages of TPS over other methods, including kriging. TPS possesses a number of robust properties: it is independent of the spatial distribution of input data, it uses a standard GIS grid structure for topographic analysis, it maintains the quality of contours, and it has consistently demonstrated flexibility and accuracy in model development. TPS is based on a minimization of interpolation-smoothing functions that possess global derivatives of all orders and include a tension parameter for controlling (smoothing) function fit to the geometric scatter of data points. A large tension parameter produces an interpolated surface with sharper points but a closer fit to actual field data. Because field data are associated with random error, this may not be desirable. A smaller tension parameter increases the smoothness of the interpolated surface. TPS is related to kriging (Wahba 1990). TPS algorithms have been developed for hydrological modeling (Mitásová and Hofierka 1993; Mitásová and Mitás 1993; Mitásová et al. 1996), and these are the ones used in this analysis. TPS may have promising applications for ecology and conservation biology in modeling the distribution and density patterns of populations or genetic structure and species-habitat relationships on landscape scales, and research along these lines is continuing.

TPS was used to model the changes in the distribution and density patterns of desert tortoise (*Gopherus agassizii*) populations after six years of landscape-scale military training activities in the central Mojave Desert (Krzysik, 1996). The research was conducted at Fort Irwin, California, the army's national training center, in 1983 and 1989. The study site was 2,600 square kilometers in size. Local patches of tortoise densities were estimated at sample quadrats of 0.64 square kilometer by sampling tortoise burrows and scats along 2.4 kilometers-by-9.1-meter triangular transects and calibrating to Bureau of Land Management permanent study plots of known tortoise densities. Transects were approximately evenly dispersed in potential habitat at the rate of one transect per 3 square kilometers of landscape. Details of field methods and background information are available in Krzysik and Woodman (1991), and statistical analysis of population trends are presented in Krzysik (1996).

Figure 42-4 is a map of Fort Irwin showing the Goldstone Deep Space Communications Complex, closed to army training and off-road vehicles (ORVs), and five impact zones. Although the impact zones are used for live-fire practice, the actual target sites are small, and most of the areas represent extensive buffer zones with high-quality habitats. Figure 42-5 shows Fort Irwin with an overlay of mountain ranges (cross-hatched pattern) and the 1989 distribution of desert tortoise populations (shaded). Compare Figure 42-5 with Figure 42-4 and note that three impact zones lie just south of the Granite Mountains and that there is an impact zone in the southeast corner of the installation.

Figure 42-6 represents the TPS surface model of the 1983 Fort Irwin tortoise population landscape, with the amplitude of the peaks representing tortoise density. Note that the orientation is southward (looking from the northern portion of the installation). This is necessary because of the high tortoise density along the southern boundary. From the northwest to the southeast, note that the locations of Gary Owen, Nelson, Lucky Fuse, and Langford impact zones are masked, because these areas in 1983 contained live, unexploded ordnance and were off-limits to tactical vehicles and tortoise surveyors. The TSP model clearly shows the high tortoise densities along the installation's southern boundary and at Goldstone, visible in the right center of the figure. Importantly, note the tortoise population along the southern bajada (ancient coalesced alluvial fans) of the Granite Mountains, including the large density peak in Granite Pass, between Lucky Fuse and Nelson (fur-

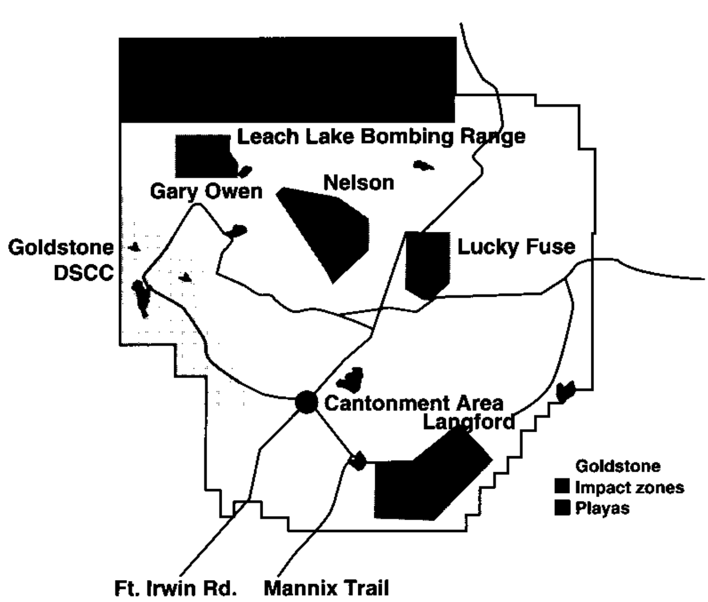

Figure 42-4. Map of Fort Irwin, California, illustrating its three management units: Leach Lake Bombing Range, Goldstone Deep Space Communications Complex, and National Training Center (rest of installation); live-fire impact zones; playas; cantonment area (housing and infrastructure); and major roads.

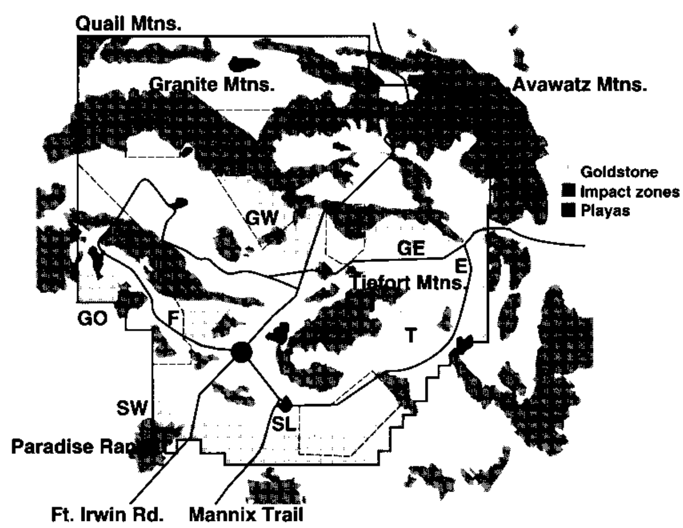

Figure 42-5. Map of Fort Irwin, California. This map is similar to Figure 42-4, with the addition of mountain ranges and the eight desert tortoise populations identified in the 1989 survey.

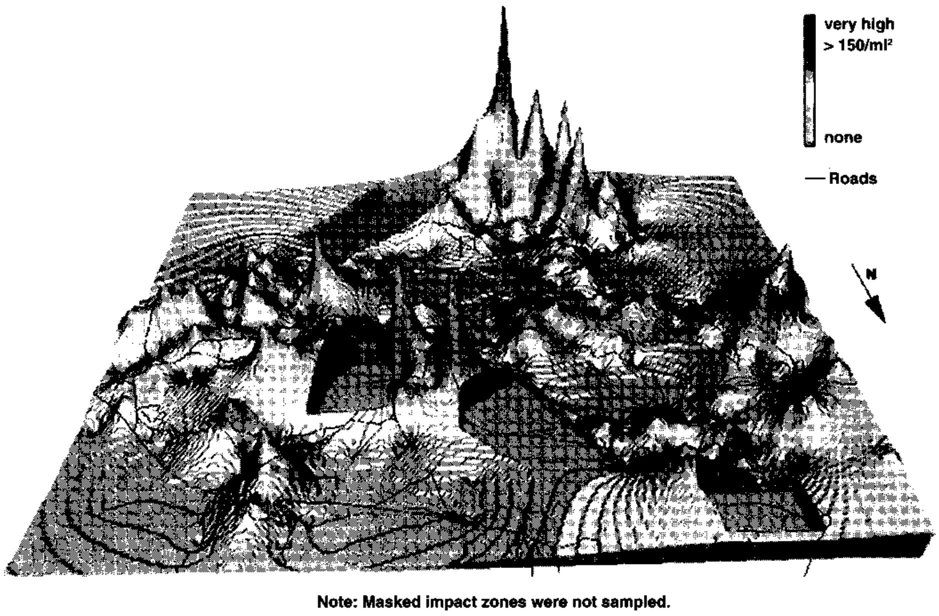

Figure 42-6. Thin-plate splines modeling tortoise density surface at Fort Irwin, California, in 1983. The orientation is toward the south. Compare with Figures 42-4 and 42-5 for pertinent landscape features. Peak amplitudes are proportional to estimated tortoise densities. Note that the impact zones are masked out because these were not cleared of hazardous ordnance until 1984 to 1985.

ther note that density peaks lie on either side of the road through this pass). Tortoises were also found in the northwest corner of the installation between Gary Owen and Goldstone and throughout the east-central valleys.

Figure 42-7 represents the TPS of the 1989 Fort Irwin tortoise populations landscape. The four impact zones were cleared of hazardous ordnance in 1984 to 1985. Note that tortoise populations along installation boundaries and at Goldstone remain viable. The population along the southern boundary extends into the former unsurveyed Langford impact zone, clearly showing a strong density peak in the extreme southeastern corner of the installation. This portion of the installation has been relatively free from tactical vehicles and represents very high quality habitat. The increased sampling effort in 1989 "exposed" the tortoise population in the Multi-Purpose Range Complex (F in Fig. 42-5), which is off-limits to tactical vehicles. The clearing of hazardous ordnance from the impact zones has enabled tactical vehicles to sweep across the landscape in the southern bajada of the Granite Mountains. Note that the former population in Granite Pass is no longer present, and the once continuous population along the southern bajada of the Granites has been fragmented into two smaller populations, GE and GW (Fig. 42-5), which have retreated higher into the bajada. A comparison of the TPS figures demonstrates the loss of tortoises in the northwestern portion and in the east-central valleys of the installation. TPS tortoise density modeling paralleled the results of the statistical analysis.

Summary

This chapter introduces the technologies and applications of Geographic Information Systems (GIS), cartography (maps), landscape ecology, and spatial modeling to field biologists and herpetologists and includes selected references on these topics. The motivation has been to inspire field herpetologists interested in assessing and monitoring amphibian populations to reflect on their research designs and needs in the context of the information presented and to acquire new interdisciplinary approaches and technologies. Concepts discussed in cartography include map scales, map projections, geographic coordinate systems, and thematic maps. Principles of GIS are developed, stressing capabilities and ap-

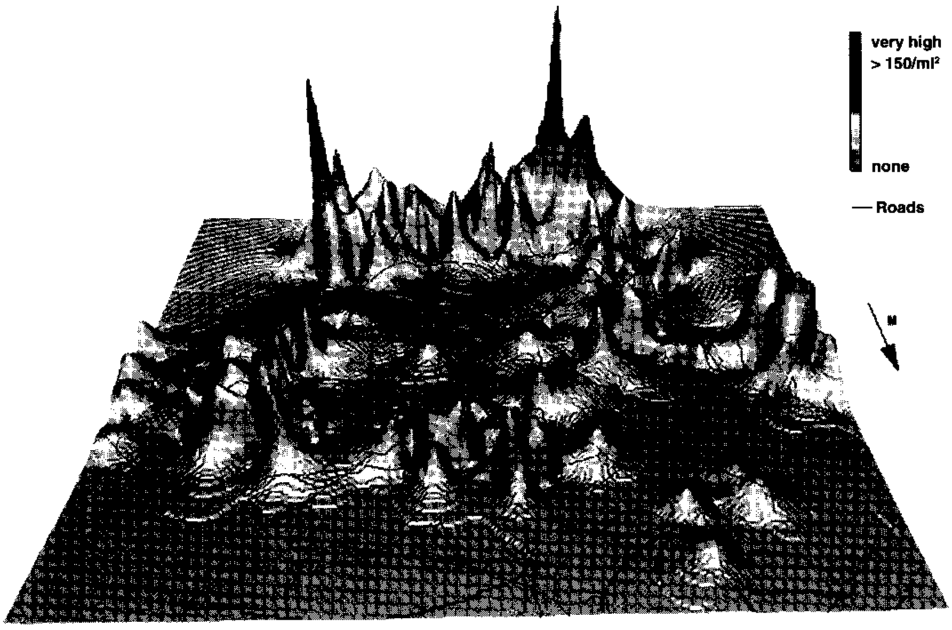

Figure 42-7. Thin-plate splines modeling tortoise density surface at Fort Irwin, California, in 1989. Note the presence of tortoises in the Langford and Nelson impact zones.

plications, nature of input data and analysis, and the relative merits of vector and raster GIS modes. GIS applications in remote sensing, landscape management and assessment/monitoring, conservation biology, and satellite telemetry are reviewed. Fundamental concepts and terminology of landscape ecology are presented, stressing quantitative aspects of landscape patterns, including issues of scale. A major discipline of spatial modeling is reviewed—interpolation and smoothing of geographic field data. An example is demonstrated using thin-plate splines for producing a landscape-scale distribution and density surface of fragmented desert tortoise populations.

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Helena Mitásová, Jocelyn Aycrigg, and Kevin Seel were instrumental in the science and art of thin-plate splines. The GIS expertise of Diane Szafoni and Jocelyn Aycrigg was important to the readability and organization of this chapter.

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13. ABSTRACT ***(Maximum 200 words)***

Natural resources and wildlife managers for Federal agency lands, including those dedicated to military training and testing missions, must make decisions at multiple scales and with implications that extend far beyond the local boundaries of the land the managers are responsible for. Although landscape management at the local level is still as important as ever, current perception for long-term ecological sustainability requires regional contexts and conservation efforts.

This document contains three peer-reviewed chapters from Status and Conservation of Midwestern Amphibians, M. J. Lannoo, editor, published by the University of Iowa Press in 1998. These chapters provide quantitative guidance and landscape perspectives to military land managers.

The first chapter describes a very fundamental approach to coarse-grained classification of ecosystems on a regional or continental basis and classifying taxa within the ecosystems.

The second chapter provides guidance to novice and experienced field biologist for designing and implementing ecological assessment or monitoring programs, and identifies important principles and issues in experimental design, field data collection, data management, and statistical analysis.

The third chapter provides an introduction to the complex and valuable technologies and applications of Geographic Information Systems (GIS), cartography, landscape ecology and its metrics, and spatial modeling.

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